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Your file Votre référence
ISBN: 978-0-494-45899-0
Our file Notre référence
ISBN: 978-0-494-45899-0

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Abstract

Animal vocalizations affect daily decision-making processes, yet selection pressures driving the evolution of communication are poorly understood. I explored two elements of communication in collared pikas (*Ochotona collaris*) in Yukon and Alaska. First, using playback experiments, I tested whether pikas 1) attended to and distinguished between alarm calls of sympatric alpine mammals, and 2) differentiated between calls of conspecifics. Pikas became alert after playback of marmot and ground squirrel alarm calls, but had more active responses to pika stimuli. In 30 habituation trials, pikas discriminated between conspecific calls, likely due to frequency differences between individuals. Listening to sympatric animals provides information about predator activity and the potential threat of individual conspecifics. Second, I examined geographic variation in pika calls. Classification trees allocated pika calls to their correct populations with 75-94% accuracy. American (*O. princeps*) and collared pika calls showed more similarity than expected given that they are distinct, allopatric species. I found no evidence that environmental adaptation caused call variation between species. Genetic divergence may drive intra- and inter-specific differences in acoustic parameters.

Acknowledgements

There are a number of individuals and organizations who helped to make this research possible. First, thank you to my supervisor Dr. David Hik for letting me take an idea and run with it, and for providing me with the opportunity to fall in love with the place we call Pika Camp. Thanks also to my committee members Dr. Chris Sturdy and Dr. Susan Hannon for very helpful ideas over the development of the project. Special thanks to the entire Sturdy lab for their help and patience while I analyzed pika calls in their sound laboratory.

To everyone who spent time at Pika Camp with me, thank you for your support and for making the whole experience both wonderful and memorable: Ryan Danby, Shawn Morrison, Matt Mitchell, Saewan Koh, Scott Wilson, Sabine Nouvet, Dorit Mersmann, James Hudson, Alex Taylor, Alana Clason, Hayley Lanier, Michaela Timciska, Isla Myers-Smith, Helen Wheeler, Vijay Patil, Françoise Cardou, Jolene Swain, Jody Pongracz, and Sylvie Mitford. Special thanks to Kieran O'Donovan and Mark Wong, for recording pika calls on the Icefields and Vulcan.

Financial and logistic support was provided by the Arctic Institute of North America (AINA), Natural Sciences and Engineering Research Council of Canada (NSERC), Canada Foundation for Innovation (CFI), DIAND Northern Scientific Training Program (NSTP), Canadian Circumpolar Institute, Steve and Elaine Antoniuk Graduate Scholarship in Northern Research, and Alberta

Ingenuity Studentship. Kluane First Nation gave permission to conduct this research on their traditional lands.

Finally, thanks to Helen, Phil, and Amy Trefry, and Geoff Holroyd, for your guidance and support.

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Chapter 1: Introduction to animal communication – setting the context for pika vocalizations

Animal Vocalization

The acoustic environment is an integral part of an animal's habitat and provides information that determines an individual's behaviour and energetic investment (Bradbury & Vehrencamp 1998). Vocalizations are a significant means of transmitting messages about the signaler or stimulus between con- and heterospecifics (e.g. Conner 1985a, Daniel & Blumstein 1998, Shriner 1998). Animal vocalizations are therefore expected to be a product of strong evolutionary selection pressures resulting from environmental and social factors (Shelley & Blumstein 2004).

Selection pressures that drive animals to emit potentially risky alarm calls have been of great theoretical interest. Shelley and Blumstein (2004) evaluated the relative importance of two adaptive, non-exclusive hypotheses for the evolution of alarm calling in 209 species of rodents. The first hypothesis was that calls are directed at predators and deter pursuit (Hasson 1991), and the second hypothesis was that calls are directed at relatives and increase direct and indirect fitness (Maynard Smith 1965, Zuberbühler et al. 1999). Given that a number of species are known to assess predation risk and call only when risk is relatively low (Wolff 1980, Blumstein & Armitage 1997), Shelley and Blumstein (2004) predicted that alarm calling species would be diurnal, and

that alarm calling driven by nepotism may exist in social species. Both diurnality and social living were significantly associated with alarm calling, but rodent alarm calling was better explained by diurnality. This suggests that alarm calling in rodents has evolved to signal caller alertness, discouraging predator pursuit (Blumstein 1999, Hasson 1991). In some species, alarm calling may also have evolved independently to warn kin of danger if the potential fitness benefits from nepotism outweigh the risk of calling (Dunford 1977, Sherman 1977).

Increasing evidence suggests that alarm calls carry a great deal of information above and beyond a warning of predator presence. For example, alarms can communicate the predator type, or the risk or urgency level (Blumstein 1995, Blumstein & Arnold 1995, Fichtel & Hammerschmidt 2002, Sloan & Hare 2004, Leavesley & Magrath 2005, Randall et al. 2005, Sloan et al. 2005). Alarm calls may also reveal group or individual identity if consistent differences between calls exist (Smith 1977, Conner 1985a).

Individually unique vocalizations have been documented in at least 136 species of birds (Stoddard 1996). Mammals and amphibians are also capable of producing individually unique calls (Hare 1998, Bee & Gerhardt 2002). Individual or group discrimination allows animals to react differently to neighbours than to strangers, and many studies have provided evidence of neighbour-stranger discrimination (e.g. Stoddard 1996, Melman & Searcy

1999, Bee & Gerhardt 2001a, 2001b, Frommolt et al. 2003, Lovell & Lein 2004, Radford 2005). Animals often react more aggressively to territorial intrusions by non-neighbours than neighbours, and this has been termed the 'dear enemy' phenomenon (Fisher 1954). Neighbour-stranger discrimination might allow an animal to advertise occupancy of a territory, and save time and energy by preventing agonistic encounters with established neighbours posing little threat (Conner 1985a). This ability can therefore minimize the energy expended on aggressive acts, and prevent escalated contests between neighbours (Ydenberg *et al.* 1988).

Animals gain information not only from the calls of conspecifics, but also heterospecifics. When co-occurring species have common predators, recognizing and responding to the alarm calls of heterospecifics may help alert individuals to predator presence and location (Shriner 1998, Rainey et al. 2004). Several species of birds and animals are known to respond to the alarm calls of co-occurring species (Moynihan 1962, Buskirk 1976, Gaddis 1980), and further evidence of interspecific alarm call recognition is demonstrated in playback experiments where animals responded to alarm calls of heterospecifics in the absence of predators (Nuechterlein 1981, Sullivan 1984, Shriner 1998, Seyfarth & Cheney 1990, Rainey et al. 2004).

Vocal Variation

Several factors often cited as causing geographic differences in vocalizations are: evolutionary divergence, acoustic adaptation to a local environment, and vocal learning (e.g. Collins & Terhune 2007, Delgado 2007, Risch et al. 2007). Population level variation in call structure in American pikas (*Ochotona princeps*) has been attributed to genetic divergence between populations with unique evolutionary histories (Sommers 1973, Conner 1982). Some of this divergence may be a result of genetic drift or population bottlenecks associated with recurrent local extinction, typical of pika metapopulations (Moilanen et al. 1998, Franken & Hik 2004). Variation may also arise due to selection pressures incurred by the physical environment. The acoustic adaptation hypothesis (AAH) assumes that structural differences between habitats will influence sound transmission, and predicts that certain types of vocalizations will transmit with less overall degradation than others in a given environment (Morton 1975). Selection pressures imposed by the acoustic environment may play a role in increased vocal variation in populations from habitats with different sound transmission properties (Daniel & Blumstein 1998). The AAH has been widely tested in birds. In a meta-analysis of evidence for the AAH in songbirds, Boncoraglio and Saino (2007) found that vegetation cover (open versus closed) weakly predicted four frequency features of bird song (maximum, minimum, peak frequency and frequency range), but had no effect on a temporal feature of songs (interval duration between notes or syllables). In contrast, there has been relatively little work

testing the AAH in mammals. Geographic vocal variation may also be attributed to animal learning, where vocalizations are modified as a result of experience with other individuals (Janik & Slater 1997). This leads to population differences in vocal signatures when individuals learn the calls of their parents or other local animals (Smith 1977). While evidence for vocal learning has been described in birds, and is particularly well documented in songbirds (Bloomfield et al. 2004), it has only been described in a few mammals. Thus far, bats, phocids (true seals), cetaceans, and primates have provided the strongest evidence for vocal learning abilities in mammals (Janik & Slater 1997). Future studies may reveal that other animals are also capable of vocal learning.

By exploring pika behavioural responses to alarm calls and the sources of geographic variation of vocalizations, the work presented here will increase our understanding of the intricacies of communication between con- and heterospecifics, as well as the potential selection pressures leading to vocal variation.

Pika Ecology

Collared pikas (*Ochotona collaris*) are small (~160 g), non-hibernating, food-hoarding lagomorphs inhabiting alpine talus (boulderfield) patches separated by meadow in the Yukon, Alaska, Northwest Territories, and northern British Columbia (Fig. 1-1, Smith 1981, Smith & Ivins 1984). The two North American

pika species are territorial and facultatively monogamous (Smith & Ivins 1984). Talus-dwelling pikas such as the collared pika are considered to exhibit a 'classic' metapopulation structure (Smith 1980, 1987; Hanski & Gilpin 1991; Smith & Gilpin 1997; Peacock & Smith 1997; Moilanen *et al.* 1998, Franken & Hik 2004). Their physical environment may create a barrier to long distance dispersal, and tagged or radio-collared pikas at our main study site in southwestern Yukon dispersed less than a kilometre away from their natal site (Franken 2002). Allozyme patterns, blood protein analysis, and loci analysis across different pika populations indicate that some populations experiencing low gene flow between patches are very homogeneous and are undergoing genetic differentiation (Brunson *et al.* 1977, Glover *et al.* 1977, Hafner & Sullivan 1995). Potential terrestrial predators of American pikas (*O. princeps*) in the southern Rocky Mountains include longtail weasels (*Mustela frenata*), short-tailed weasels (*M. erminea*), and pine martens (*Martes americana*). At our main study site in the Yukon, short-tailed weasels are present and have been observed hunting collared pikas. Other potential predators observed include Golden eagles (*Aquila chrysaetos*), Short-eared owls (*Asio fammeus*), American kestrels (*Falco sparverius*) and Merlins (*Falco columbarius*).

Pikas provide an excellent opportunity to study questions about animal communication. In the summer months when they are 'haying', or making food caches for the winter, they are easily observed, call frequently and repeatedly, are territorial and therefore easy to relocate, and become habituated to human

presence (Smith 1974, Conner 1983b, Dearing 1996, Beever et al. 2003). The pikas at our study site are marked with metal ear tags and coloured wire and are therefore individually identifiable (Fig. 1-2).

Pika Vocalizations

The function of collared pika calls has received relatively little attention, however, studies on calls of the closely related American pika (*O. princeps*) suggest two main functions: as a predator warning and as a territorial defense (Ivins & Smith 1983, Conner 1985a). Ivins and Smith (1983) investigated the responses of American pikas to terrestrial predators, and suggested that calls functioned to warn neighbouring pikas, often kin. They proposed that it is unlikely that calls were directed at predators, since weasels were observed to hunt more actively for pikas after hearing calls. Pikas modified their calling behaviour based on predator type, calling less frequently and after a longer delay to weasels compared to martens (Ivins & Smith 1983). The function of pika calls as a response to predators was further supported by Hayes and Huntly (2005). Pikas became less active under windy conditions when calls may attenuate more rapidly or become distorted, thereby decreasing their effectiveness as a predator warning (Hayes & Huntly 2005). In other contexts, calls deter conspecifics from intruding into a territory and stealing vegetation from a neighbour's haypile (Conner 1985a, Dearing 1997, Morrison 2007). Unlike some marmot species (Blumstein 1999), pikas do not appear to have different calls for unique situations or degrees of risk. Collared pika calls, given

in response to predators and in territorial defense, sound the same to the human ear.

Vocalizations maintain and define social relationships in many organisms (e.g. Esser 1994, Bradbury & Vehrencamp 1998, Robbins 2000, Insley 2000). Collared pika vocalizations almost certainly function as a primary mechanism for establishing and maintaining social organization, particularly as individuals who are aggressive for much of the year must come together to breed in the spring beneath the snow. Contact signals are likely necessary for establishing and maintaining pair bonds, and dictating breeding behaviour in pikas (Conner 1985b). American pikas produce nine distinct acoustic signals. The evolution of this call diversity, which is much more extensive than that exhibited by other lagomorphs, has been attributed to pikas' atypical social organization and the visually disruptive environment in which they live (Conner 1985b). For pikas, individual recognition of calls may be important to social interactions when haying and moving through other pika's territories, when foraging at territory boundaries, during the breeding season to allow identification of potential mates, and in directing aggression and altruistic behaviours such as alarm calling (Conner 1985b, Franken 2002). Franken and Hik (2004) found that dispersal in collared pikas is critical to maintain the metapopulation structure in which they live. Franken (2002) suggested that in collared pikas, hearing highly vocal individuals defending their territories likely influences other pikas when making dispersal and settlement decisions. Thus, environmental and

social selection pressures have probably directed the call structure of pikas in a variety of ways. Gaining insight into these influencing factors will increase our knowledge of the evolution of animal communication in alpine environments.

Conner (1985a) studied individually marked American pikas from two populations in Colorado. Pikas had individually distinct call structures, and responded differently to naturally occurring calls given by different individuals and to playbacks of familiar versus unfamiliar calls. The significant differences in responses indicated that American pikas were able to discriminate between individual callers by sound alone (Conner 1985a). Pikas on one talus responded more strongly to familiar calls, while on a second talus pikas responded more strongly to unfamiliar calls, which may be a result of the history of the two populations and differences in the levels of competition for space between the two locations (Conner 1985a). The calls of Japanese pikas may also carry information about individual identity (Kojima et al. 2006). American pikas, therefore, may be able to make decisions about energy expenditure and behavioural response based on the identity of a caller (Conner 1983a, 1985a). Decisions about the time spent creating haypiles, or food caches, in late summer can be critical to over-winter survival in pikas (Dearing 1997, Morrison 2007). The prevalence of kleptoparasitism of neighbours' haypiles attests to the importance of this winter resource

(McKechnie et al. 1994). Any mechanism, such as call recognition, that would increase the time dedicated to haying would be advantageous (Conner 1985).

Study Area

The main study site was located in a sub-arctic alpine meadow in the Ruby Ranges, southwest Yukon (Fig. 1-3, 61°12'N, 138°16'W; 1700-2100 m). This area is a 4 km^2 valley, with talus patches ranging in size from 0.07 to 17.7 ha interspersed between expanses of meadow (Fig. 1-4). The vegetation type is alpine tundra, dominated by *Dryas octopetala*, *Salix reticulata*, graminoids, and lichens. Collared pikas have been trapped and monitored at this site since 1995. Other herbivores in the valley include hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Spermophilus parryii*). All three species use vocal alarm signals.

In the Yukon, collared pikas were recorded in the main study valley and adjacent valleys (Fig. 1-5), and at Tombstone Territorial Park (6°28'N, 139°47'W; 1461 m), Mount Decoeli (60°49'N, 137°50'W; 1435 m), Vulcan Mountain (60°56'N, 138°32'W; 1903m, Fig. 1-6), St. Elias Icefields (60°32'N, 139°25'W; 1887 m), and in Alaska along the Denali Highway (63°04'N, 146°13'W; 1188 m, Fig. 1-7, Fig. 1-8). American pikas (Fig. 1-9) were also recorded at several sites in Jasper, Alberta (Fig. 1-10).

Recording Equipment

Recordings were made using a Marantz Professional Solid State digital recorder (Model PMD671, Mahwah, NJ, USA) and an Audio Technica microphone (Model AT835b, Broadcast & Production Microphones, Stow, OH, USA, frequency response 40 to 20000 Hz, signal-to-noise ratio 70 dB; Fig. 1-11A). In all playback experiments, calls were broadcast through Altec Lansing in Motion iM4 speakers (Milford, Pennsylvania, frequency response 60 Hz to 20 kHz; Fig. 1-11B) from an iPod mini (Apple Inc., Cupertino, CA, USA). Limitations of the recording setup included that ultrasound (>20 kHz) could not be measured, and that I had to be quite close to an animal to capture high quality recordings. This, however, made it easier to target individuals, particularly when marked. The number of individual playback stimuli used was limited by the time taken to acquire high quality recordings, and the amplitude of playbacks had to be low enough to avoid distortion when projected through the speakers.

Research Goals

The first goal of this study was to determine the extent to which pikas use the vocalizations of con- and heterospecifics to gain information about their environment, through playback experiments presented in Chapter 2. I predicted that pikas would respond to alarm call playbacks of both con- and heterospecifics with vigilant behaviour (e.g. raising head to look for a predator, calling), but that pikas would react more strongly to the alarm calls of

conspecifics, which are more likely to announce predators that are of significant threat to pikas (e.g. weasels, Ivins & Smith 1983) or territorial invasions (Conner 1984). I also wanted to determine if pikas would 1) discriminate between the calls of different individual conspecifics and 2) respond differently to calls from different distances from their haypiles. I predicted that pikas would be able to discriminate between individual callers due to the potential energetic benefit this would confer, and that they would respond most strongly to the calls of strangers and least strongly to established neighbours posing less of a threat to the pika's own territory (Conner 1985a). With respect to the origin of the playback call, I predicted that pikas would respond more strongly to a pika call next to their haypiles than a pika call farther away due to the increased level of perceived threat to their territory or haypile via kleptoparasitism (McKechnie *et al.* 1994).

The second goal of this study was to sample pika calls from geographically separate populations, and to explore call variation between populations, using classification trees, and individuals (Chapter 3). I also sampled vocalizations of the closely related American pika, the only other pika species in North America, in order to assess the degree of interspecific call variation. Recorded pika calls from our main study site provided me the opportunity to determine whether certain call characteristics might carry information about individual identity. Finally, I tested whether acoustic adaptation has played a role in call divergence between the two species. This study is an important initial attempt

at determining the sources of geographic call differences in pikas, and will aid in understanding the mechanisms leading to vocal variation. It may also increase our understanding of pika metapopulation dynamics, if differences in call structure are a result of genetic relatedness (Conner 1983a).

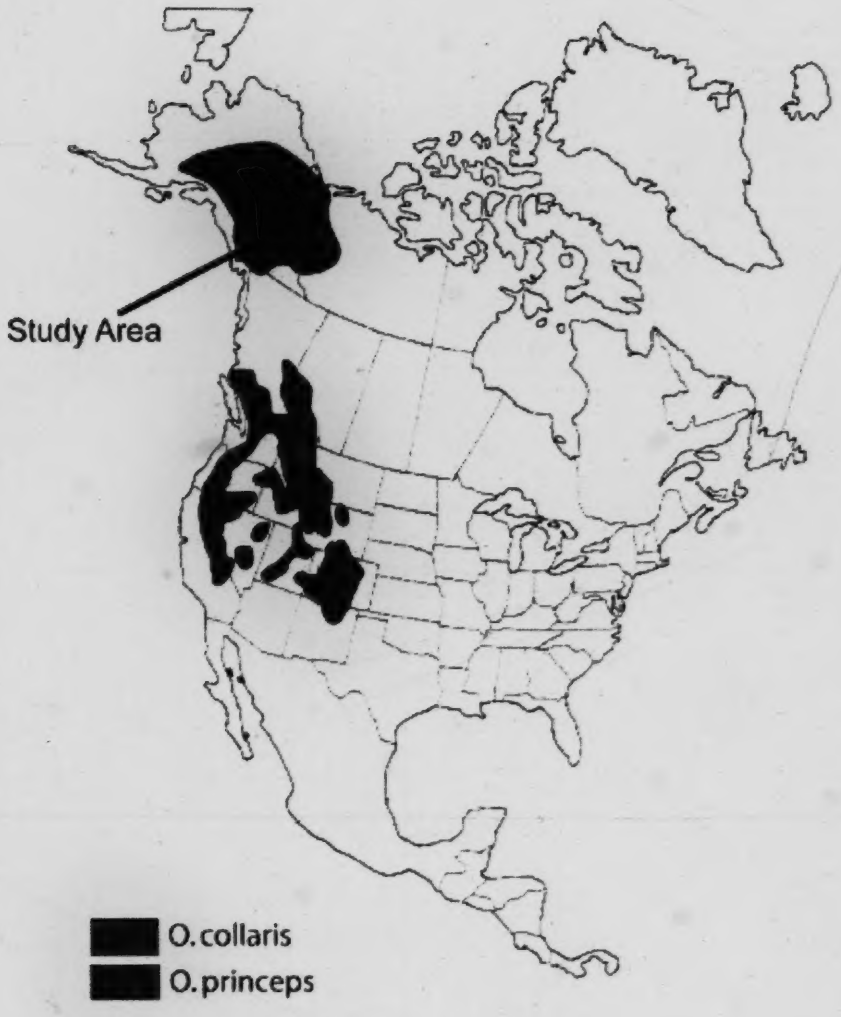

Figure 1-1. Species range of collared (*O. collaris*) and American (*O. princeps*) pikas. Image modified from Smith et al. (1990).

Figure 1-2. Collared pika (*Ochotona collaris*) with metal ear tag and coloured wire for individual identification.

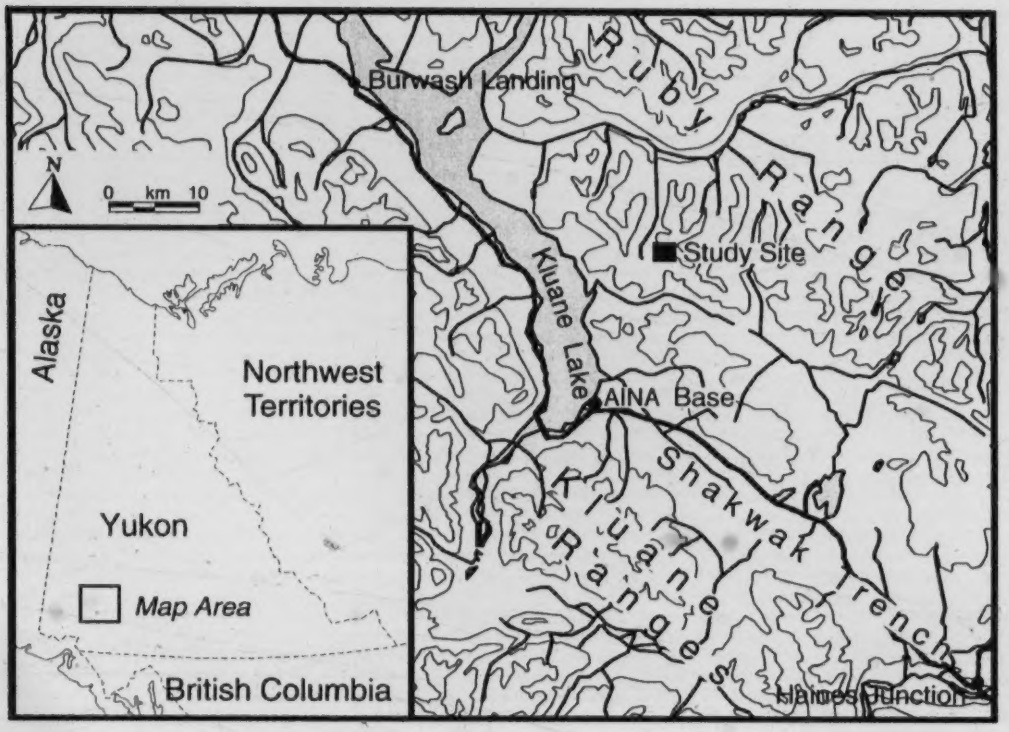

Figure 1-3. Location of study site east of Kluane Lake in the Ruby Range, southwest Yukon. Image © R. Danby.

Figure 1-4. Pika Camp, the main study site in the Ruby Ranges, southwest Yukon.

Figure 1-5. Valley of the Five Lakes, collared pika recording site in the Ruby Range Mountains, Kluane, Yukon.

Figure 1-6. Vulcan Mountain, collared pika (*Ochotona collaris*) recording site in the Front Range, southwestern Yukon.

Figure 1-7. Collared pika (*Ochotona collaris*) recording site along the Denali Highway, Alaska.

Figure 1-8. Recording collared pikas (*Ochotona collaris*) along the Denali Highway, Alaska. Photo © M. Peterson.

Figure 1-9. American pika (*Ochotona princeps*) in Jasper, Alberta. Photo © H. L. Dickson.

Figure 1-10. Collared pika (*Ochotona collaris*) recording site in Jasper, Alberta.

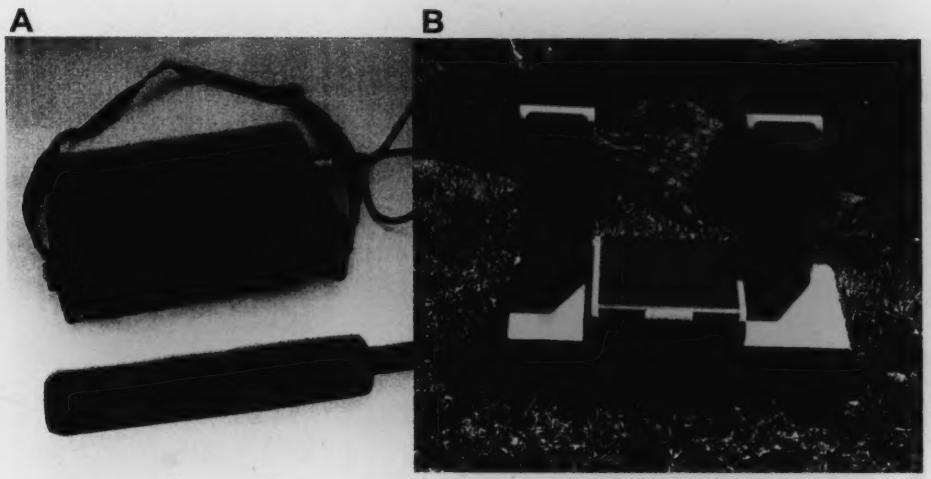

Figure 1-11. Recording and playback equipment. **A**) Marantz Professional Solid State digital recorder (Model PMD671, Mahwah, NJ, USA) and Audio Technica shotgun microphone (Model AT835b, Broadcast & Production Microphones, Stow, OH, USA). **B**) Altec Lansing in Motion iM4 speakers (Milford, Pennsylvania, frequency response 60 Hz to 20 kHz).

References

Beever, E.A., P.F. Brussard, & J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy **84**:37-54.

Bloomfield, L.L., I. Charrier, & C.B. Sturdy. 2004. Note types and coding in parid vocalizations. II: The chick-a-dee call of the mountain chickadee (*Poecile gambeli*). Canadian Journal of Zoology **82**:780-793.

Blumstein, D.T. 1995. Golden-marmot alarm calls. I. The production of situationally specific vocalizations. Ethology **100**:113-125.

Blumstein, D.T. 2005. The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling. In: *Rodent societies*. Wolff, J.O. & P.W. Sherman (eds). Chicago, University of Chicago Press.

Blumstein D.T. & K.B. Armitage. 1997. Alarm calling in yellow-bellied marmots, 1: the meaning of situationally variable alarm calls. Animal Behavior **53**:143–171.

Blumstein, D.T. & Arnold, W. 1995. Situational specificity in alpine marmot alarm communication. Ethology **100**:1-13.

Blumstein, D.T., L.Verneyre & J.C. Daniel. 2004. Reliability and the adaptive utility of discrimination among alarm callers. Proceedings of the Royal Society of London B **271**:1851-1857.

Boughman, J. W. & G.S. Wilkinson. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. Animal Behaviour **55**:1717-1732.

Bradbury, J.W., S.L. Vehrencamp. 1998. *Principles of Animal Communication.* Sunderland, Massachusetts, Sinauer Associates, pp. 1-11, 571-615.

Brunson, J.T., R.N. Seaman, and D.J. Nash. 1977. Interpopulational variation of blood proteins in pika (*Ochotona princeps saxatilis*). Great Basin Naturalist **37**:77-80.

Buskirk, W.H. 1976. Social systems in a tropical forest avifauna. American Naturalist **110**:293-310.

Collins, K.T. & J.M. Terhune. 2007. Geographic variation of Weddell seals (*Leptonychotes weddellii*) airborne mother-pup vocalizations. Polar Biology **30**:1373-1380.

Conner, D.A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy **63**:48-52.

Conner, D.A. 1983a. Response of pikas to playback of geographic variations of the short call. Journal of Mammalogy **64**:336-337.

Conner, D.A. 1983b. Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). Canadian Journal of Zoology **61**:411-416.

Conner, D.A. 1985a. The function of the pika short call in individual recognition. Journal of Comparative Ethology **67**:131-143.

Conner, D.A. 1985b. Analysis of the vocal repertoire of adult pikas: ecological and evolutionary perspectives. Animal Behaviour **33**:124-134.

Daniel, J.C. and D.T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour **56**:1517-1528.

Dearing, M.D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. Oecologia **108**:467-478.

Dearing, M.D. 1997. The function of haypiles of pikas (*Ochotona princeps*). Journal of Mammalogy **78**:1156-1163.

Delgado, R.A. 2007. Geographic variation in the long calls of male orangutans (*Pongo* spp.). Ethology **113**:487-498.

Dunford, C. 1977. Kin selection for ground squirrel alarm calls. American Naturalist **111**:782–785.

Dusenbery, D.B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information.* New York, W.H. Freeman.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist Supplement **139**:125-153.

Esser, K.H. 1994. Audio-vocal learning in a nonhuman mammal-the lesser spear-nosed bat *Phyllostomus discolor*. Neuroreport **5**:1718-1720.

Fichtel, C. 2002. Responses of redfronted lemurs to experimentally modified alarm calls: evidence for urgency-based changes in call structure. Ethology **108**:763-777.

Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process.* Huxley, J., A.C. Hardy, & E.B. Ford, London, Allen & Unwin, pp. 71-83.

Forrest, T.G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. American Zoologist **34**:644-654.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. thesis, University of Alberta.

Franken, R.J. & Hik, D.S. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology **73**:889-896.

Gaddis, P. 1980. Mixed flocks, accipiters, and antipredator behavior. Condor **82**:348-349.

Glover, D.G., M.H. Smith, L. Ames, J.Joule, & J.M. Dubach. 1977. Genetic variation in pika populations. Canadian Journal of Zoology **55**:1841-1845.

Grayson, D.K. 2005. A brief history of Great Basin pikas. Journal of Biogeography **32**:2103-2111.

Hare, J.F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. Animal Behaviour **55**:451-460.

Hasson O, 1991. Pursuit deterrent signals: the communication between prey and predator. Trends in Ecology and Evolution **6**:325–329.

Hafner, D.J. & R.M. Sullivan. 1995. Historical and ecological biogeography of nearctic pikas (Lagomorpha: Ochotonidae). Journal of Mammalogy **76**:302-321.

Handford, P. 1988. Trill rate in the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. Canadian Journal of Zoology **66**:2658-2670.

Hanski, I. & Gilpin, M.E. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society **42**:3-16.

Hartwig, S. 2005. Individual acoustic identification as a non-invasive conservation tool: an approach to the conservation tool: an approach to the conservation of the African wild dog *Lycaon pictus* (Temminck, 1820). Bioacoustics-The International Journal of Animal Sound and its Recording **15**:35-50.

Hayes, A.R. and N.J. Huntly. 2005. Effects of wind on the behaviour and call transmission of pikas (*Ochotona princeps*). Journal of Mammalogy **86**:974-981.

Insley, S.J. 2000. Long-term vocal recognition in the northern fur seal. Nature **406**:404-405.

Ivins, B.L. & A.T. Smith. 1983. Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. Behavioural Ecology and Sociobiology **13**:277-285.

Janik, V.M. & P.J.B. Slater. 1997. Vocal learning in mammals. Advances in the study of Behaviour **26**:59-99.

Kojima, N., K. Onoyama & T. Kawamichi. 2006. Year-long stability and individual differences of male long calls in Japanese pikas *Ochotona hyperborean yesoensis* (Lagomorpha). Mammalia **70**:80-85.

Leavesley, A.J., & R.D. Magrath. 2005. Communicating about danger: urgency alarm calling in a bird. Animal Behaviour **70**:365-373.

Leger, D.W., S.D. Berney-Key & P.W. Sherman. 1984. Vocalizations of Belding's ground squirrels (*Spermophilus beldingi*). Animal Behaviour **32**:753-764.

Maurello, M.A., J.A. Clarke, & R.S. Ackley. 2000. Signature characteristics in contact calls of the white-nosed coati. Journal of Mammalogy **81**:415-421.

Maynard Smith J, 1965. The evolution of alarm calls. American Naturalist **99**:59–63.

McKechnie, A.M., A.T. Smith, & M.M. Peacock. 1994. Kleptoparasitism in pikas (*Ochotona princeps*): theft of hay. Journal of Mammalogy **75**:488-491.

Moilanen, A., A.T. Smith & I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. The American Naturalist **152**:530-542.

Morrison, S.F. & D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology **76**:899-907.

Morton, E.S. 1975. Specific distinctiveness in the communication signals of birds. Behaviour **11**:13-39.

Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Miscellaneous Collections **143**:1-140.

Nuechterlein, G.L. 1981. 'Information parasitism' in mixed colonies of western grebes and Forster's terns. Animal Behaviour **29**:985-989.

Randall, J.A., B. McCowan, K.C. Collins, S.L. Hooper & K. Rogovin. 2005. Alarm signals of the great gerbil: Acoustic variation by predator context, sex, age, individual, and family group. Journal of the Acoustical Society of America **118**:2706-2714.

Risch, D., C.W. Clark, P.J. Corkeron, A. Elepfandt, K.M. Kovacs, C. Lydersen, I. Stirling, & S.M. Van Parijs. 2007. Vocalizations of male bearded seals, *Erignathus barbatus*: classification and geographical variation. Animal Behaviour **73**:747-762.

Robbins, R.L. 2000. Vocal communication in free-ranging African wild dogs (*Lycaon pictus*). Behaviour **137**:1271-1298.

Seyfarth, R. & D. Cheney. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. Animal Behaviour **40**:754-764.

Shelley, E.L., & D.T. Blumstein. 2004. The evolution of vocal alarm communication in rodents. Behavioral Ecology **16**:169-177.

Sherman, P.W. 1977. Nepotism and evolution of alarm calls. Science **197**:1246–1253.

Shriner, W.M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour **55**:529-536.

Sloan, J.L., & J.F. Hare. 2004. Monotony and the information content of Richardson's ground squirrel (*Spermophilus richardsonii*) repeated calls: tonic communication or signal certainty? Ethology **110**:147-156.

Sloan, J.L., D.R. Wilson, & J.F. Hare. 2005. Functional morphology of Richardson's ground squirrel, *Spermophilus richardsonii*, alarm calls: the meaning of chirps, whistles and chucks. Animal Behaviour **70**:937-944.

Smith, A.T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology **55**:1368-1376.

Smith, A.T. 1980. Temporal changes in insular populations of the pika (*Ochorona princeps*). Ecology **60**:8-13.

Smith, A.T. 1981. Population dynamics of pikas. In: *Proceedings of the World Lagomorph Conference*. Myers, K. & C.D. MacInnes (eds), Guelph, Ontario, Guelph University Press.

Smith, A.T. 1987. Population structure of pikas: dispersal versus philopatry. In: *Mammalian Dispersal Patterns: the Effects of Social Structure on Populaiton Genetics*, Chepko-Sade, B.D. & A.T. Halpin (eds), Chicago, University of Chicago Press, pp.128-142.

Smith, A.T. & M. Gilpin. 1997. Spatially correlated dynamics in a pika metapopulation. In: *Metapopulation Biology: Ecology, Genetics and Evolution*, Hanski, I.A. & M.E. Gilpin (eds), New York, Academic Press.

Smith, A.T. & B. L. Ivins. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Journal of Comparative Ethology **66**:289-308.

Smith, A.T. & M.L. Weston. 1990. *Ochotona princeps*. Mammalian Species **352**:1-8.

Smith, A.T., N.A. Formozov, R.S. Hoffmann, C. Zheng, & M. Erbajeva. 1990. Rabbits, Hares, and Pikas: Status Survey and Conservation Action Plan. In: *The Pikas*, Chapman, J.A., & J.E.C. Flux (eds), Gland, Switzerland, IUCN, pp. 14-60.

Sommers, P.L. 1973. Dialects in southern Rocky Mountain pikas *Ochotona princeps* (Lagomorpha). Animal Behaviour **21**:124-137.

Smith, W.J. 1977. *The Behaviour of Communicating: An Ethological Approach*. Cambridge, Massachusetts, Harvard University Press, pp. 343-388.

Stoddard, P.K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds.* Kroodsma, D.E., & E.H. Miller (eds), New York, Cornell University Press, pp. 356-373.

Sullivan, K. 1984. Information exploitation by downy woodpeckers in mixed-specis flocks. Behaviour **91**:294-311.

Wei-Dong, L. & A. T. Smith. 2005. Dramatic decline of the threatened Ili pika *Ochotona iliensis* (Lagomorpha: Ochotonidae) in Xinjiang, China. Oryx **39**:30-34.

Wiley, R.H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. American Naturalist **138**:973-993.

Wiley, R.H. & D.G. Richards. 1978. Physical constrains on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behaviourla Ecology and Sociobiology **3**:69-94.

Wiley, R.H. & D.G. Richards. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds.* Kroodsma, D.E., E.H. Miller, & H. Ouellet, New York, Academic Press, pp. 131-181.

Wolff, J.O. 1980. Social organization of the taiga vole (*Microtus xanthognathus*). The Biologist **62**:34.

Ydenberg, R.C., L.A. Giraldeau, & J.B. Falls. 1998. Neighbours, strangers, and the asymmetric war of attribution. Animal Behaviour **36**:343-347.

Zuberbühler K., D. Jenny, R. Bshary. 1999. The predator deterrence function of primate alarm calls. Ethology **105**:477–490.

Chapter 2: Eavesdropping on the neighbourhood: Responses of collared pikas (*Ochotona collaris*) to playback calls of con- and heterospecifics

INTRODUCTION

Animals derive information about their surroundings from a variety of sources, including the local acoustic environment. Major contributors to the acoustic environment are the vocalizations of sympatric species (e.g. Conner 1985, Daniel & Blumstein 1998, Shriner 1998). Alarm calls are one type of vocalization thought to have evolved to either communicate directly to predators to deter an attack (Hasson 1991), or to warn conspecifics of predators (Maynard Smith 1965, Zuberbühler et al. 1999). Evidence supporting the hypothesis of direct communication to predators suggests that some vocalizations in birds and mammals act as pursuit-deterrent signals (Cresswell 1994, Shelley & Blumstein 2004). Recent studies suggest that most rodent alarm calls evolved to communicate to predators, while in other species nepotism may explain the persistence or independent evolution of alarm calls (reviewed in Shelley & Blumstein 2004).

Alarm calls may provide detailed information about the caller, the predator, or the degree of risk perceived by the caller. For example, golden-marmots (*Marmota caudata aurea*) and alpine marmots (*Marmota marmota*) produce alarm calls that vary in the number of notes with predator type or risk level

(Blumstein 1995, Blumstein & Arnold 1995). Such specificity can inform receivers more precisely about predators in their environment.

The specific information gained from vocalizations also depends on the perceptual abilities of the listener. Many species are able to discriminate between the calls of neighbours versus strangers (e.g. Stoddard 1996. Melman & Searcy 1999, Bee & Gerhardt 2001), and often react more aggressively to territorial intrusions by non-neighbours versus neigbours. This has been termed the 'dear enemy' phenomenon (Jaeger 1981, Ydenberg et al. 1988, Temeles 1994). Distinguishing calls of established residents versus potentially threatening strangers can prevent escalated conflict between neighbours and minimize energy expended on aggressive acts (Ydenberg et al. 1988). Consistent differences between individuals' calls can lead to a refined level of discrimination (Bradbury & Vehrencamp 1998). Individually unique vocalizations have been documented in many birds (Stoddard 1996), and mammals and amphibians also produce them (Hare 1998, Bee & Gerhardt 2002). The evolution of individual recognition may be driven by factors such as the cost of aggressive encounters (Hardouin et al. 2006), by differences in caller reliability (Cheney & Seyfarth 1988, Hare & Atkins 2001, Blumstein et al. 2004), or as a means of assessing kinship (Hare 1998, Hare & Atkins 2001).

The ability to interpret and respond to alarm calls of con- and heterospecifics is advantageous when sympatric species share common predators (Fichtel 2004). Shriner (1998) found that yellow-bellied marmots (*M. flaviventris*) and golden-mantled ground squirrels (*Spermophilus lateralis*) living with shared predators in eastern California responded similarly to playback of con- and heterospecific anti-predator calls. Other playback experiments have indicated that several species of birds, rodents, and primates respond to alarm vocalizations of co-occurring species in the absence of predators (e.g. Nuechterlein 1981, Shriner 1998, Seyfarth & Cheney 1990). The extraction of information from signaling interactions by individuals not directly involved has been termed 'eavesdropping' (Peake et al. 2005). By eavesdropping on the vocalizations of other species, individuals can be alerted to the presence, location, and size of predators (Shriner 1998, Rainey et al. 2004, Templeton & Greene 2007).

In this study I documented the behavioural responses of collared pikas (*Ochotona collaris*, Lagomorpha) living in southwest Yukon to playback of con- and heterospecific calls. The information gained from eavesdropping on alarm calls of other species has gone relatively unstudied, particularly in mammals. Exploring pikas' responsiveness to alarm calls increases our knowledge about the evolution and development of anti-predator mechanisms and active assessment within and between species (Shriner 1998). While vocalizations of collared pikas have not been previously investigated, studies on the closely

related American pika (*O. princeps*) have indicated two main functions of calls: as a predator alarm and for territory defense (Somers 1973, Conner 1982, Ivins & Smith 1983, Conner 1985, Hayes & Huntly 2005). The vocalizations of American pikas are distinct enough to allow individual recognition, and also differ geographically (Conner 1982, 1985).

Three playback experiments were conducted to determine whether collared pikas use the vocalizations of con- and heterospecific mammals to obtain information about their environment. Experiment 1 explored whether pikas attend to alarm calls of heterospecific alpine mammals. I predicted that if pikas share common predators with other alpine mammals, particularly avian predators such as Golden Eagles (*Aquila chrysaetos*), they would respond to recordings of hoary marmot (*Marmota caligata*) and Arctic ground squirrel (*Spermophilus parryii*) alarm calls with vigilant behaviour (e.g. actively looking for predators, calling), but that they would respond more strongly to alarm calls of conspecifics, since the latter are more likely to announce predators specific to pikas (e.g. short tailed weasels, *Mustela erminea*) or the threat of territorial invasion (Conner 1984). In Experiment 1, I also tested whether pikas would respond differently to conspecific calls from two different distances from their winter food cache, or haypile. Calls given closer to a pika may be perceived as denoting a more imminent threat of territorial invasion or of predator attack. My objective in Experiments 2 and 3 was to determine whether pikas could distinguish between individual callers. If energetic benefit is construed through

individual recognition via the 'dear enemy' hypothesis, I predicted that pikas would discriminate between individual callers and would respond more strongly to the calls of strangers than neighbours. Stranger calls may be perceived as more threatening since, unlike established neighbours, strangers might be seaking to acquire a territory and haypile for themselves (Conner 1985). Experiment 3 is a habituation experiment similar to one described by Evans (1997) and carried out by Weiss and Hauser (2002), used to demonstrate individual discriminatory abilities.

GENERAL METHODS

Study Organism

Collared pikas are small (~160 g), non-hibernating, food-hoarding lagomorphs inhabiting alpine boulderfields in the Yukon, Alaska, Northwest Territories, and northern British Columbia (Smith 1981, MacDonald & Jones 1987). They are territorial and facultatively monogamous, inhabiting spatially isolated patches of talus separated by alpine meadows (Smith & Ivins 1984, Franken & Hik 2004). Pikas provide an excellent opportunity to study questions about animal communication. In the summer months when they are making food caches for the winter ("haying"), they are easily observed, call frequently and repeatedly, are territorial and therefore easy to locate, and quickly become habituated to human presence (Smith 1974, Conner 1983, Dearing 1996, Beever et al. 2003).

Collared pikas use the same acoustic signal as both an alarm and in territorial defense, indicating that the information extracted from calls is contingent on the context in which they are broadcast (Smith 1965, 1977). Leger (1993) defined call context as the set of events, conditions, and changeable recipient characteristics that modify the effect of a signal on a recipient's behaviour. Therefore, it is likely that pikas attending to conspecific alarm calls are actively extracting not only signal-related information, but also information from contextual sources. Because pika calls sound the same to the human ear when given in either context, it was often difficult to determine the reason an individual was calling when recording pikas in the field. Since the context was often unknown and may not always have been given to alert other animals to danger, I refer to pika vocalizations as 'calls' rather than 'alarm calls'.

Study Site

The study site is located in the Ruby Range, southwest Yukon (61°12'N, 138°16'W; 1700-2100m), in a 4 km^2 valley with typical pika habitat of talus patches (boulderfields), interspersed by expanses of meadow (Franken & Hik 2004, Fig. 2-1). The vegetation was alpine tundra, dominated by *Dryas octopetala*, *Salix reticulata*, graminoids, and lichens. Collared pikas have been trapped and monitored at this site since 1995 (Morrison & Hik 2007), and marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire for identification from a distance.

Acoustic Stimuli Acquisition and Transmission

Local vocalizations of mammals and birds were recorded using a Marantz Professional Solid State digital recorder (Model PMD671, Mahwah, NJ, USA, frequency response 40 to 20000 Hz), at a sampling rate of 44100 Hz and 16-bit sample/s, and a shotgun microphone (Model AT835b, Audio Technica, Broadcast & Production Microphones, Stow, OH, USA). Arctic ground squirrels and hoary marmots are two of the most vocal animals that co-occur with pikas, and all three species often give alarm calls simultaneously in response to potential predators. Golden-crowned sparrows (*Zonotrichia atricapilla*) are common in the valley. I used golden-crowned sparrow songs as a control stimulus to eliminate the possibility that pikas responded to an aspect of the playback protocol or equipment. When necessary, vocalizations were bandpass filtered using RAVEN 1.2.1 (Cornell Lab of Ornithology, Biouacoustics Research Program, Cornel, NY, USA) for Mac OS X to reduce ambient sound not associated with the animal calls, particularly wind. Bandpass frequencies used were: 2500-6200 kHz for golden-crowned sparrow songs, 2600-15000 kHz for Arctic ground squirrel alarm calls, and 1700-16000 kHz for hoary marmot alarm calls (Fig. 2-2). The bandpass frequencies used differ between species in order to isolate the call and remove the most background sound possible, without altering elements of the call itself. Pika calls were not filtered due to their broad bandwidth. Recordings used as stimuli had little background noise, strong amplitude, and captured the entire

bandwidth of the animal's audible call below 20 kHz (ultrasound was not recorded).

Calls were broadcast in a randomized sequence through Altec Lansing in Motion iM4 speakers (Milford, Pennsylvania, frequency response 60 Hz to 20 kHz) from an iPod mini (Apple Inc., Cupertino, CA, USA) to 30 individual pikas in each experiment. Pika responses were quite uniform within-stimulus type and did not appear to be affected by playback order. Twenty pikas were used in both Experiment 1 and 2 (details of each follow in next section). Exposure to the call of a stranger from Experiment 1 may have diminished the response to a stranger in Experiment 2. To minimize this effect, Experiment 2 trials were conducted more than a week after the end of Experiment 1, and different individuals were recorded as stranger stimuli for use in the second Experiment. There did not appear to be a diminished response by pikas previously exposed to the playbacks in the second Experiment. Experiments 1 and 2 were carried out between 21 June and 7 August 2006, with an average of two trials conducted per day. Experiment 3 was conducted between 8 and 17 August 2007, averaging three trials per day. Trials conducted on the same day occurred on distinct talus patches separated by meadow, so that pikas did not hear stimuli prior to a trial in which they were the target pika. In all three experiments, two 10 X 16 cm feeding trays made of wire supported by two wooden struts were baited with *Salix barclayi* and *Petasites frigidus*, and placed in an individual pika's territory, on talus and near the haypile for all but

the 'pika-far' stimulus. After a pika emptied the feeding tray, they were replenished at least once before the trial began. Sound stimuli were only presented to pikas when they were foraging from the feeding trays. I sat 10-20 m away from the feeding trays. Pikas were allowed to visit the trays several times before a call was played, in order to establish a standard baseline behaviour from which the response to calls could be determined.

EXPERIMENT 1: PIKA RESPOINSES TO SYMPATRIC ANIMAL VOCALIZATIONS

Methods

The first Experiment tested pika responses to heterospecific alarm calls and near and far conspecific calls. Sound stimuli were created from recordings taken within ten meters of an animal. These consisted of i) hoary marmot flat calls, which are used more frequently than ascending or descending calls and multinote trills (Blumstein & Armitage 1997) and were given in response to naturally occurring predators at our study site, ii) arctic ground squirrel "chatter" vocalizations (Melchior 1971, Banfield 1974), often emitted from the burrow entrance as an animal was approached by a human, and iii) the songs of golden-crowned sparrows (Holmes & Dirks 1978). Collared pika calls were also recorded 2.5 km from our main study site to create 'stranger' stimuli.

Having multiple stimuli exemplars is important if individual variation exists between callers (Blumstein & Armitage 1997). While it is ideal to have a

unique individual caller for each trial (Kroodsma et al. 2001), the number of exemplars of each stimulus was limited by the time required to acquire these prior to the study. Therefore, recordings from five golden-crowned sparrows, six hoary marmots, eight arctic ground squirrels, and fifteen collared pikas were used sequentially as stimuli throughout the trials. All stimuli were projected at a volume of 64-70 dB, measured at 2 m from the speakers using a Radio Shack digital sound level meter (Model # 33-2055, A weighting, fast). Calls were not normalized (e.g. Frommolt et al. 2003, Blumstein & Daniel 2004, Christie et al. 2004, Blumstein & Munos 2005), so sound pressure levels reflect the natural variance between individuals and species. Sound pressure level also varies with recording distance, which was minimized by maintaining a distance of 10 m or less between the microphone and animal when recording stimuli. Call stimuli were composed of strings of repeated exemplars lasting approximately 20 seconds, in series that approximate the pauses between naturally occurring calls. Golden-crowned sparrow stimuli were comprised of 6 songs lasting 2.1 seconds on average, with 3 seconds of silence between repeated songs. Ground squirrel stimuli consisted of 6 calls lasting an average of 0.21 seconds, with 2 seconds between calls. Six 0.82-second alarm calls were used to create the hoary marmot stimuli, and 0.10-second pika calls were repeated 10 times, separated by 3 seconds of silence. The target pika was exposed to each type of stimulus over the course of a trial.

Two sets of speakers were set up; one on talus 5-10 m from the feeding trays (pika-near stimulus), and one off talus (in meadow) 15-20 m away from the feeding trays (pika-far stimulus). The heterogeneity of the environment and the proximity of neighbours in many cases precluded having speakers farther from the feeding trays and on talus. This setup therefore reflects the natural environment, where calls from neighbours are often transmitted first over meadow and then over talus. The stimuli presented in a randomized sequence were i) the flat call of a hoary marmot, ii) the alarm chatter of an arctic ground squirrel, iii) the call of a collared pika 'stranger' played from near (5-10 m speakers) and iv) from farther away (15-20 m speakers), and v) a golden-crowned sparrow song. All heterospecific stimuli were presented through the speakers 5-10 m from the haypile. Stimuli were presented to adult pikas: 15 males, 10 females, and 5 pikas of undetermined sex.

Behavioural Response Categories

Conner (1983) showed that different American pika behavioural responses could be used to measure discrimination of playback of different calls. The behavioural response of collared pikas following each playback stimulus was recorded for two minutes following the call, although responses were usually immediate. These response behaviours were categorized on a scale from zero to seven (Table 2-1). Initially no assumptions about the 'strength' of pika responses were made. However, with the exception of "yawning", the categories may represent a gradient of responses from weak to strong.

"Yawning" was an additional category added because this behaviour was observed after trials began (see Discussion).

Statistical Analysis

Pika responses were divided into "action responses", indicating pika movement, and "vocal responses", indicating pika vocalizations and "yawns". Action and vocal responses were not mutually exclusive, and were analyzed separately, so that a pika might have both an action and vocal response for each stimulus, but not more than one response in either category. G-tests of independence with a Williams' correction for small sample size were used to determine whether pika responses were contingent on stimuli, followed by post hoc pairwise comparisons. Because multiple paired comparisons were conducted, a Bonferroni correction was applied to these tests, and effects are reported at a 0.017 significance level. In all cases, doing the correction did not significantly alter the p-values. Odds ratios are reported to aid interpretation.

Results

Pikas heard and responded to playback stimuli in a manner comparable to observations of pikas responding to naturally occurring vocalizations. Action responses were contingent on stimulus type (golden-crowned sparrow, hoary marmot, arctic ground squirrel, pika-near and pika-far, $G=3436.64$, $df=16$, $p<0.001$, Fig. 2-3). However, pika action responses did not differ between the pika-near and pika-far stimuli ($G=6.19$, $df=5$, $p>0.25$), nor to the marmot and

ground squirrel stimuli (action response: $G=1.68$, $df=4$, $p>0.50$). Therefore, action responses fell into three general classes of predominant behaviour: pikas did not respond to sparrow calls, they raised their heads in response to marmot and ground squrrel calls, and they moved towards the speakers in response to conspecific calls. Vocal responses were not contingent on stimulus ($G=3.45$, $df=8$, $p>0.90$). Vocal responses were generally less frequent than action responses, particularly as a response to heterospecific stimuli (Fig. 2-3). Odds ratios reflect the different responses to stimuli; pikas were 8 times more likely to raise their head in response to ground squirrel and marmot calls than to pika calls. Pikas were 110 times more likely to move towards the speakers and twice as likely to call in response to pika stimuli than to ground squirrel and marmot stimuli. Adult male ($n=15$) and female ($n=10$) pikas did not respond differently to playback stimuli in either their action ($G=3.43$, $df=4$, $p>0.25$) or vocal ($G=3.99$, $df=2$, $p>0.10$) responses.

EXPERIMENT 2: PIKA RESPONSES TO CONSPECIFIC CALLS

Methods

The second experiment tested pika responses to different individual callers. Pika calls were recorded in calm conditions from 5-10 m away. Stimuli consisted of the target pika's own call, their nearest neighbour, next nearest neighbour, a 'stranger' from 2.5 km away, and the song of a golden-crowned sparrow, used as a control stimulus. In high population density years, like the summer of 2006, distance between neighbours was approximately 30-70 m

(Franken 2002). The 'stranger' stimulus was recorded at a distance well beyond the mean dispersal distance of juveniles at our site (Franken 2002).

A single set of speakers was set up 5 m from the feeding trays, on talus. The stimuli presented in a random sequence were: 1) the target pika's own call ("self"), 2) the nearest neighbour's call, 3) the next nearest neighbour's call, 4) a strange pika's call, and 5) the song of a golden-crowned sparrow. Stimuli were again presented to adult pikas: 16 males, 11 females, and 3 pikas of undetermined sex.

Behavioural Response Categories

The same behavioural response codes from zero to seven used in Experiment 1 were also used in Experiment 2 (Table 2-1).

Statistical Analysis

Experiment 2 was analyzed using the same method as the first experiment, where pika responses were divided into non-exclusive "action" and "vocal" categories and analysed using G-tests of independence with a Williams' correction.

Results

Both pika action ($G=1726.61$, $df=16$, $p<0.001$) and vocal responses ($G=1353.19$, $df=16$, $p<0.001$) were contingent on stimulus type (Fig. 2-4).

However, this was due to differences in pika responses to the golden-crowned sparrow song compared with all other pika stimuli, and pikas responded similarly independent of which pika stimulus they heard. Though this experiment was designed to determine whether collared pikas could discriminate between individual conspecific callers, the uniformity of their responses to pika stimuli made this difficult to assess. Pikas were 95 times more likely to have no response to golden-crowned sparrow songs than to pika stimuli.

Both action ($G=13.90$, $df=4$, $p<0.001$) and vocal ($G=8.11$, $df=2$, $p<0.05$) responses were contingent on pika gender (n=15 males and 11 females; Fig. 2-5). Odds ratios reflect these differences: females were 4 times more likely to perch than males, and males were 3 times more likely to move greater than half the distance to the speakers as females. In Experiment 2, males were 15 times more likely to "yawn" than females in response to pika stimuli.

EXPERIMENT 3: PIKA RESPONSES TO CONSPECIFIC CALLS FOLLOWING HABITUATION

Methods

The final Experiment consisted of a series of habituation trials to test more precisely whether pikas could discriminate between the calls of two different individuals. Pika calls recorded for Experiment 2 in 2006 were used to create 20 stimulus pairs of two pikas. Since 30 trials were conducted, ten stimulus

pairs were used twice. Eleven stimulus pairs consisted of pikas from opposite sides of the valley, and nine pairs from the same side (Table 2-2, Fig. 2-2). For pairs where both sexes were known, four were both sexed as male, one both female, and three pairs had a male and female caller. Pikas were not presented with their own calls.

A single set of speakers was set up ≤5 m from the feeding trays. Stimuli presented consisted of two pika calls, from two individuals: A and B. Once the target pika was foraging from the trays, a single call from pika A was played, followed by a five second pause, then repeated calls from pika B at three second intervals, which continued until the target pika had habituated (i.e., stopped responding to the call). After a five second pause, pika A was played a second time. In ten control trials to ensure that the five second pause was not causing a renewed reaction to the second playback of pika A following habituation, pika B was played a final time after a five second pause ("B_{test}") (See below for visual representation of trial stimuli). Playing pika A before habituating the target pika to Pika B's call ensured that pikas were not responding differently to call B after habituation simply because the caller was a different individual. If pikas renew vigilance on hearing a second pika call after habituation to the first call, then they are able to discriminate between pika A and B. Conversely, if pikas do not de-habituate after the second call of individual A, they may lack discriminatory abilities.

habituation trial playback order (N=30):

A_1---$^{5sec\ pause}$---B_1-$^{3\ sec\ pause}$-B_2-$^{3\ sec\ pause}$-B_3.....A_2

habituation control playback order (N=10):

A_1---$^{5sec\ pause}$---B_1-$^{3\ sec\ pause}$-B_2-$^{3\ sec\ pause}$ -B_3.....B_{test}

Behavioural Response Categories

Behavioural responses were classed as 0 (not vigilant: foraging, sleeping), 1 (low vigilance: grooming, "yawning", licking, chewing, scent marking), and 2 (vigilant: moving around speakers, calling). Broader categories were used than in playback Experiments 1 and 2 because I was interested in knowing whether a pika had habituated or not, reflected in a variety of behaviours. Pika behaviour was recorded continually during the trials, grouped by minute.

I further explored the occurrence of "yawn" behaviour exhibited in all playback experiments. Richardson's ground squirrels (*Spermophilus richardonii*) produce an ultrasonic alarm call, or "whisper call", that appears to a human observer as a silent call (Wilson & Hare 2004). The possibility that pikas might be emitting ultrasound when "yawning" was investigated by placing a 240X Ultrasound detector (Pettersson Elektronik AB, Dag Hammarsjolds, Sweden) set between 30-95 kHz 0.5 to 5 m from seven pikas who emitted over twenty "yawns" and multiple calls

Statistical Analysis

G-tests of independence with a Williams' correction for small sample size were used to determine whether pika responses were contingent on stimuli, followed by post hoc pairwise comparisons. A Bonferroni correction was applied to these tests, and effects are reported at a 0.01 significance level. Doing the correction did not significantly alter the p-values. Odds ratios are reported.

Results

The frequency of each response class (vigilant, low vigilance, and not vigilant) was contingent on the stimulus presented to pikas over the course of the playback trial ($G=1241.11$, $df=8$, $p<0.001$; Fig 2-6). This was also the case in the control trials ($G=1241.11$, $df=8$, $p<0.001$). Pikas responded differently to stimuli B_1 and B_{end} ($G=5988.79$, $df=2$, $p<0.001$), indicating that pikas habituated over the course of the trial. Habituation occurred within 40 minutes on average, after approximately 800 repetitions of the same call. Pikas renewed their state of vigilance (dehabituated) after habituation when the second call of pika A was played (pairwise comparison: B_{end} and A_2, $G=314.86$, $df=2$, $p<0.001$), to the same level as the initial response to pika A (pairwise comparison: A_1 and A_2, $G=5.53$, $df=2$, $p>0.05$), indicating that pikas do discriminate between two individual calls. Pika responses were not contingent on whether they were responding to A_1 or B_1, ($G=1.40$, $df=2$

$p>0.25$), indicating that pikas had similar initial responses to both pika stimuli. Pikas did not habituate simply due to the playback design, since a pause followed by playback of pika B did not cause pikas to dehabituate (i.e. responses to B_{end} and B_{test} were identical). Overall, pika resonses to the playback trials were remarkably uniform (see Fig. 2-6). Males and females had similar responses ($G=0.033$, $df=2$, $p>0.5$).

I explored the occurrence of "yawns" that occurred during Experiment 3 trials. Pikas often approached the playback speakers before yawning, after hearing the call of a conspecific. Over the course of all three experiments, 21 males "yawned" 112 times, and 9 females "yawned" 37 times, giving an odds ratio of males nearly 3 times more likely to "yawn" in any given trial than females. Males gave a disproportionate number of "yawns" in response to hearing another male's call when sex of both caller and receiver was known (Fig. 2-7). Since this study was not designed to address this question the sample sizes of sexes are unequal. No ultrasound was detected during these observations, but under similar conditions, arctic ground squirrels produced ultrasound from 20-60 kHz while they made both alarm "whistles" and "chatter" calls (Melchior 1971).

DISCUSSION

Experiment 1: Pika Responses To Sympatric Animal Vocalizations

The most frequent responses of pikas to stimuli can be categorized into three classes: no response to the bird song, raised head in response to hoary marmot and arctic ground squirrel alarm calls, and moved towards speakers after conspecific calls. That pikas did not differentiate their responses to the pika-near and pika-far stimuli may indicate that pika calls are categorized similarly, independent of distance, until further contextual information is gained (Smith 1965, 1977; Leger 1993). Pikas responded vocally to all mammal alarm calls, which supports the notion that pikas vocalize in both a territorial context and as a predator warning, though in this experiment pikas vocalized more frequently in response to conspecifics than heterospecifics. The dual functionality of their call increases the need for pikas to seek contextual information regarding the motive for calling.

Pikas raised their heads in response to hoary marmot and arctic ground squirrel calls, and appeared to become vigilant after hearing these alarm calls. Pikas appeared to actively assess the calls of heterospecifics to gain information about shared predators. Therefore, this member of the lagomorph family shares the ability with birds, rodents, and primates to 'eavesdrop', gaining information from the vocalizations of other species. In the field, I have heard marmots, ground squirrels, and pikas call in response to grizzly bear (*Ursos arctos*), wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), and raptors

(golden eagles, peregrine falcons (*Falco peregrinus*), and American kestrels (*Falco sparverius*)), some of which are potentially shared predators of these three mammals. Being aware of and responding to the vocalizations of other alpine mammals with alarm calls provides an additional information source about a pika's environment. Common predator pressure may be a sufficient driver to warrant the evolution of recognition of heterospecific alarm calls (Fichtel 2004). This may lead to associational learning, where individuals learn to attend to such alarm calls to gain information about predator presence (Shriner 1998). Heterospecific response to playback may also be due to interspecific territoriality (Möller 1992), especially if pikas, marmots, and ground squirrels compete for similar forage species. In contrast with softer, short distance calls such as food calls that elicit begging or chipping given by flocking birds, long distance signals, such as alarm calls, are often broadcast into the public domain. While they are primarily directed at conspecifics, vocalizations inherently also invite eavesdropping by heterospecifics (McGregor & Dabelsteen 1996).

Experiment 2: Pika Responses To Conspecific Calls

Pikas responded more overtly to the playback stimuli of pika calls in both Experiments 1 and 2 than to marmots and ground squirrels in Experiment 1, often by moving towards the speakers and calling. Responses to conspecific calls were likely more pronounced than those to heterospecific alarm calls for two reasons. First, while marmots and ground squirrels may share some avian

predators with pikas, individuals may only receive warning of the presence of predators specializing on pikas from conspecifics. Ivins and Smith (1983) determined that weasels are effective predators of American pikas. At this study site, short-tailed weasels (*Mustela erminea*) appear to be one of the main predators of collared pikas, and were the only species observed to capture pikas in the summers of 2006 and 2007. Pikas call repeatedly when weasels are present, but marmots and ground squirrels at our study site do not seem to give alarm calls in response to weasels. This may indicate that weasels are not major predators of the larger mammals. That pikas reacted more actively to conspecific compared to heterospecific calls may indicate that territorial maintenance is an important function of collared pika calls. Pikas may react strongly to conspecific calls to avoid territorial intrusion (Conner 1984) or kleptoparasitism of haypiles (McKechnie et al. 1994), by letting conspecifics know that they are present on their territory. By this mechanism, calls may function to reduce more costly intraspecific encounters (Conner 1985, Ydenberg et al. 1988). After hearing conspecific calls, males were more likely to approach the speakers, while females more often perched on a rock. This may reflect a higher level of aggression or territorial defense in males. Lower levels of overt territorial aggression in females may be in part attributed to their tolerance of their own pups on their territories following emergence, and pre-dispersal.

Pika behaviour did not differ in response to playback calls of different individual pikas, whether the stimulus was the target pika's own call, its two nearest neighbours, or a strange pika. Discrimination between neighbours and strangers is expected to reduce energy expenditure through the "dear enemy" effect, where animals minimize potentially costly agonistic encounters (Temeles 1994). Similar behavioural responses to different callers does not reflect an inability to distinguish between callers; rather it may indicate an adaptive response to calls that can be given in both a territorial display and as a predator warning. Listeners may react in a similar way, independent of caller identity, until further information is gained about the context in which the call has been given. Because Experiment 2 did not provide conclusive evidence about individual discriminatory ability, I followed up with a habituation-style playback experiment.

Experiment 3: Pika Responses to Conspecific Calls Following Habituation

Collared pikas at this study site had a very uniform response to the habituation trials; they responded strongly to the calls of two conspecifics, became habituated to the second call after approximately 40 minutes, and then renewed their vigilant behaviour when the first pika was played a second time. This indicated that pikas were able to discriminate between the calls of the two pikas; if they could not, pikas would have remained habituated to the second playback of the first pika call. This renewed vigilance was not due to the pause

in the experiment design, because pikas in control trials retained a low level of vigilance following a pause.

Individual discrimination of alarm calls is known in vervet monkeys, *Cercopithecus aethiops* (Cheney & Seyfarth 1988), juvenile Richardson's ground squirrels, *Spermophilus richardsonii* (Hare 1998), yellow-bellied marmots, *Marmota flaviventris* (Blumstein & Daniel 2004), American pikas, *O. princeps* (Conner 1985), and now collared pikas (this study). I predicted that collared pikas would be able to discriminate between individual callers given the energetic benefits associated with this ability, particularly for a territorial species. Another indication that pika calls may carry enough information to allow individual coding is that frequency measures exhibit greater variation between individuals than within (see Chapter 3). If pika alarm calls were an adaptation to warn a potential predator that they have been spotted, there would be little selection pressure to distinguish individual callers (Shelley & Blumstein 2004). Given the risk that calling seems to pose in terms of detection by predators (Ivins & Smith 1983) and the results here indicating that collared pikas can discriminate between individual callers, pika calls given in a predator context likely function to alarm conspecifics of predator activity.

"Yawn" Behaviour

Females and males had similar responses to playbacks of con- and heterospecifics in all three playback experiments, but males were more likely

to "yawn", and did so more frequently than females. "Yawning" was observed repeatedly after playbacks of pika calls. An animal would move towards the playback speakers, stop, and open its mouth, with no audible sound emitted. Grooming of the face and whiskers often followed.

Many animals give yawns in different social contexts. For example, dogs may yawn as a sign of fear or anxiety, while macaques and other primates may yawn as a sign of 'uneasiness' or as a threat display (Deputte 1994, Frank et al. 2007). Yawning in several studies of non-human primates has been much more frequent in males than females, and has been linked closely to blood testosterone levels (reviewed in Deputte 1994). "Yawns" may be a behavioural response to discourage a potential invading pika that is heard very close to an individual's territory. It is also possible that "yawning" stimulates secretion of cheek glands, which in American pikas are used for scent marking (Harvey & Rosenberg 1960), play a role in breeding behaviour, and likely contribute to territory maintenance (Meaney 1983, 1986). The grooming behaviour observed following "yawning" would transfer secretions onto a pika's feet, and subsequently moving around their territories would leave a scent trail. When the sex of the stimulus pika was known, males gave "yawns" more frequently to male callers, but future studies exploring whether this behaviour is contingent on the gender of the listener and caller would help to determine the function of "yawning".

CONCLUSIONS

Collared pikas used their acoustic neighbourhood, consisting of con- and heterospecific calls, to gain information about their environment, but reacted more strongly to conspecific calls. Pikas had similar responses to the calls of different individuals but were apparently able to distinguish between callers. These behaviours have likely arisen because of the additional knowledge gained about the presence of shared predators from attending to heterospecific alarm calls, and the energetic advantage gained through individual discrimination in these territorial mammals, so that neighbours can be tolerated without disruption of foraging behaviour. The ability to discriminate between individual callers may further aid in decision-making affecting foraging, predator avoidance, and nepotism. Similar behavioural responses to conspecific calls may represent a standard adaptive response to gain further information about call context. Collared pika calls are important in both territory maintenance and as a predator warning. The dual functionality of their vocalizations gives the context of pika calls an even greater significance than in species with multiple call types. Future work exploring how animals gather contextual information from calls and the prevalence of eavesdropping between heterospecifics will further clarify the importance and evolution of interspecific communication.

Table 2-1. Response codes used to categorize collared pika (*Ochotona collaris*) behavioural responses to playback stimuli.

Response Code	Response Observed
0	No response, pika continued haying
1	Pika stopped haying and raised head from feeding trays
2	Pika stopped haying, looked up from feeding trays, and ran to a rock perch
3	Pika stopped haying, looked up from feeding trays, and ran less than half the distance to the speakers
4	Pika stopped haying, looked up from feeding trays, and ran more than half the distance to the speakers
5	Pika stopped haying, looked up from feeding trays, and called once
6	Pika stopped haying, looked up from feeding trays, and called repeatedly
7	Pika "yawned", added after trials began and this behaviour was observed. Pikas opened their mouths wide, with no apparent sound emitted. Face grooming often followed.

Table 2-2. Summary of location and sex of pikas recorded for stimuli used in the habituation experiment in the southwest Yukon. Pikas were presented in the order A_1, B_1, B_2, B_3.....A_2, where letters refer to calls from different individual pikas and the subscript refers to the number of times the call was played. M=male, F=female.

Stimulus pair	Location: pika A	Location: pika B	Sex: pika A	Sex: pika B
1	Camp Creek	West Side	unknown	M
2	Camp Creek	West Side	M	M
3	Camp Creek	West Side	F	unknown
4	East Side	West Side	M	M
5	East Side	West Side	F	F
6	East Side	West Side	M	F
7	East Side	West Side	F	M
8	East Side	West Side	F	unknown
9	East Side	West Side	M	F
10	East Side	West Side	F	unknown
11	East Side	West Side	M	M
12	Greenhouses	West Side	unknown	unknown
13	Greenhouses	West Side	unknown	M
14	Hawaiian Islands	West Side	unknown	M
15	Hawaiian Islands	Hawaiian Islands	M	unknown
16	Hawaiian Islands	Hawaiian Islands	F	unknown
17	Camp Creek	Hawaiian Islands	M	M
18	East Side	East Side	F	unknown
19	West Side	West Side	M	unknown
20	West Side	West Side	F	unknown

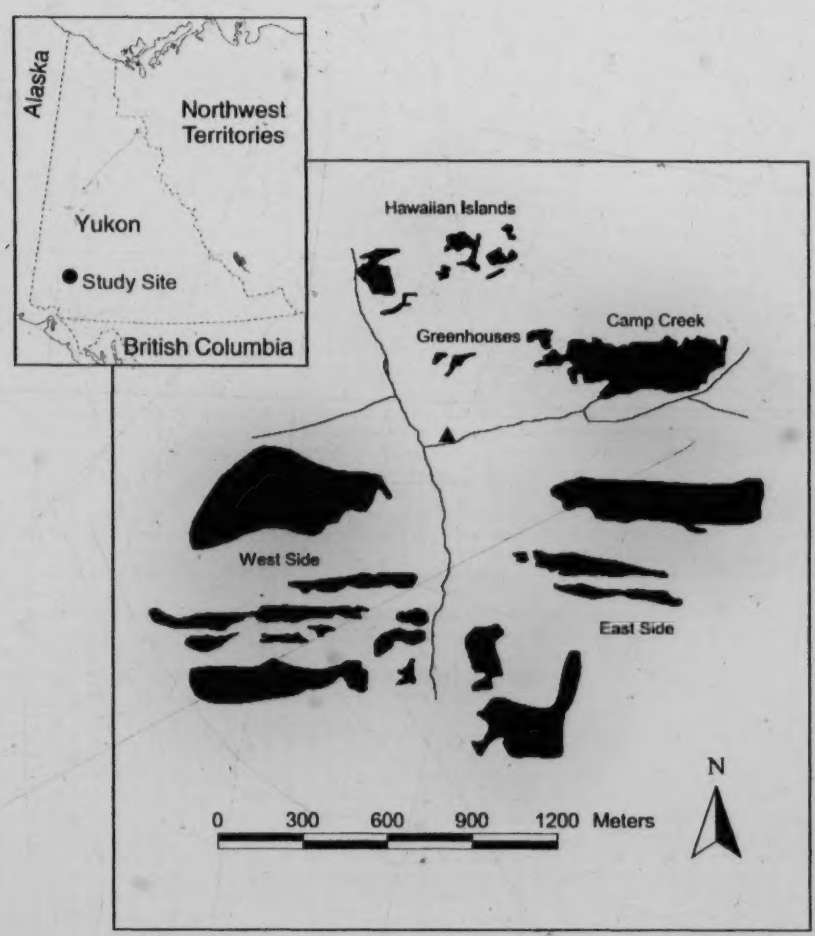

Figure 2-1. Talus patches at our main study site in the Ruby Ranges, Yukon. Black areas represent talus (boulderfields) surrounded by meadow (white). Lines are creeks. Triangle represents the camp site. Adapted from Franken (2002).

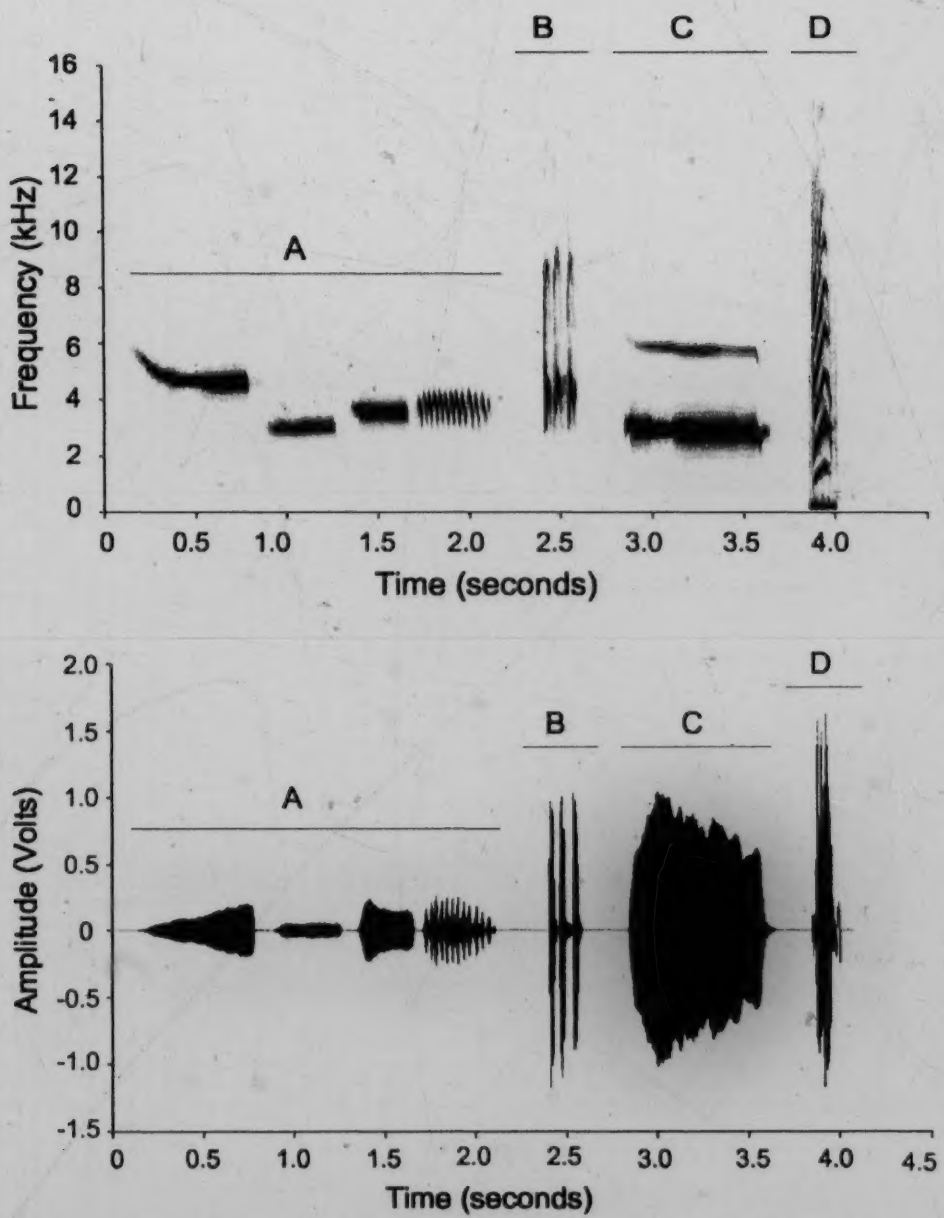

Figure 2-2. Spectrogram (top) and spectrum (bottom) of exemplar of each stimulus used in playback experiments. A: Golden-crowned sparrow (*Zonotrichia atricapilla*), B: Arctic ground squirrel (*Spermophilus parryii*), C: hoary marmot (*Marmota caligata*), D: collared pika (*Ochotona collaris*).

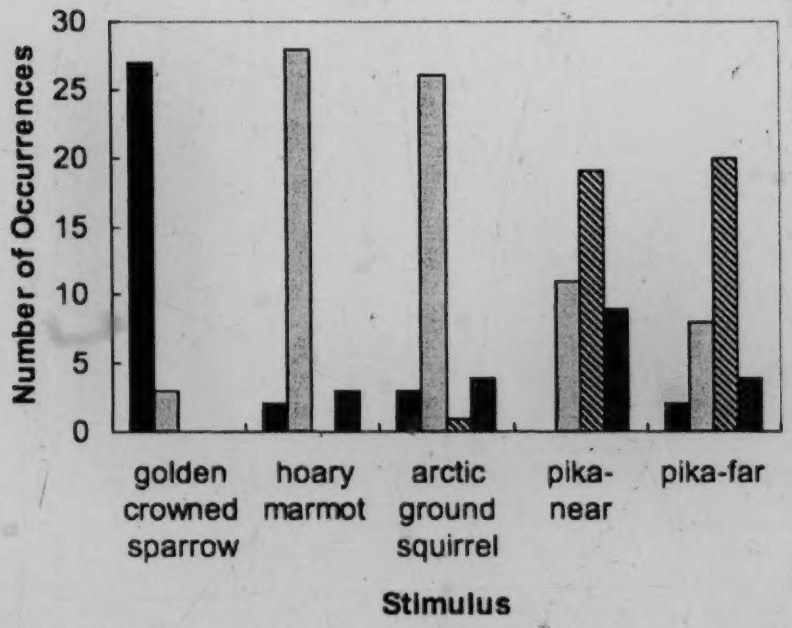

Figure 2-3. Responses of 30 collared pikas (*Ochotona collaris*) to playback stimuli of sympatric animal vocalizations. ■ = no response, □ = raise head (action response), ▨ = move towards speakers (action response), ■ = vocal response.

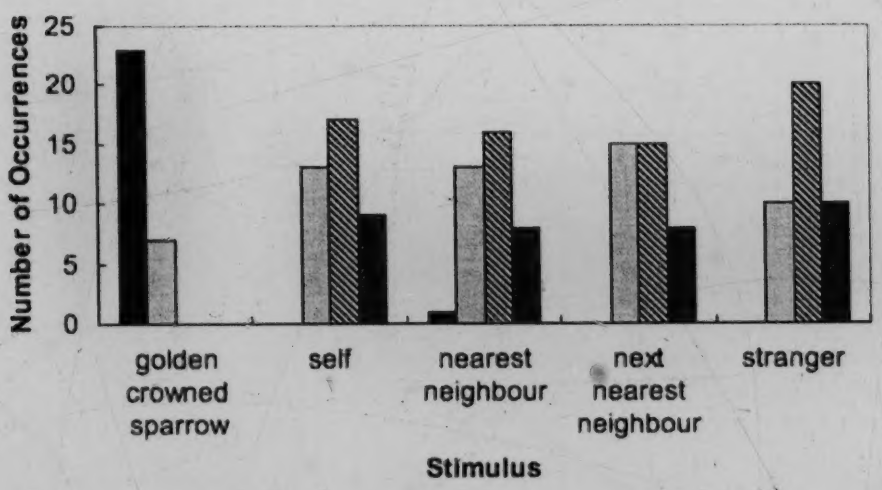

Figure 2-4. Responses of 30 collared pikas (*Ochotona collaris*) to playback stimuli of a golden-crowned sparrow song and conspecific calls (self=pika's own call, stranger=pika recorded ~2.5km from target pika). ■= no response, ▨= raise head (action response), ▧= move towards speakers (action response), ■= vocal response.

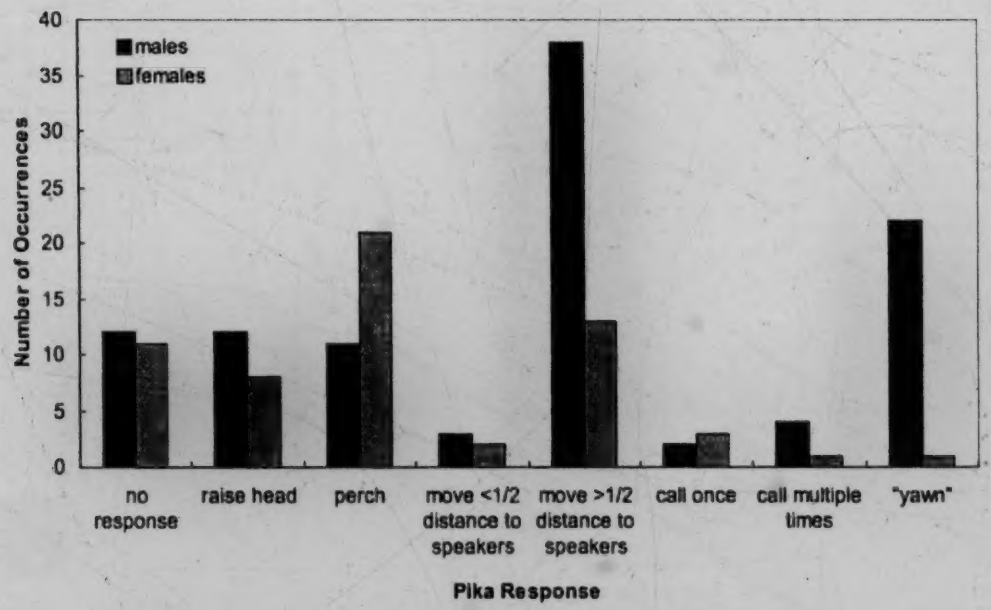

Figure 2-5. Responses of male and female collared pikas (*Ochotona collaris*) to playbacks of pika stimuli (their own call, two nearest neighbours' calls, and a stranger's call).

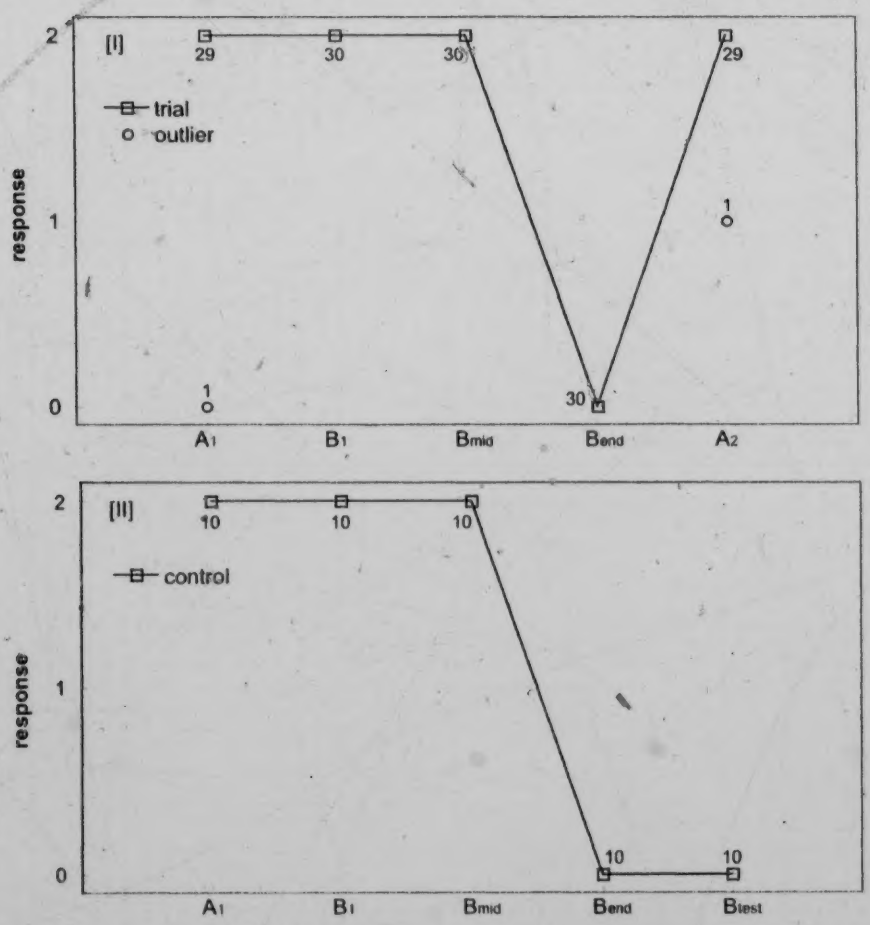

Figure 2-6. [I] Responses of collared pikas (*Ochotona collaris*) to playbacks of call A from pika-1, followed by call B from pika-2 played until habituation. 0-not vigilant (foraging), 1=low vigilance (grooming, scent marking), 2=vigilant (alert, calling). Subscript numbering indicates first or second playback of call, mid and last indicate middle or end of habituation period. Values next to points represent number of animals exhibiting response. N_{trial}=30. [II] In control trials call B was repeated after a 5 sec pause, to ensure renewed vigilance was not a result of experimental design. $N_{control}$=10.

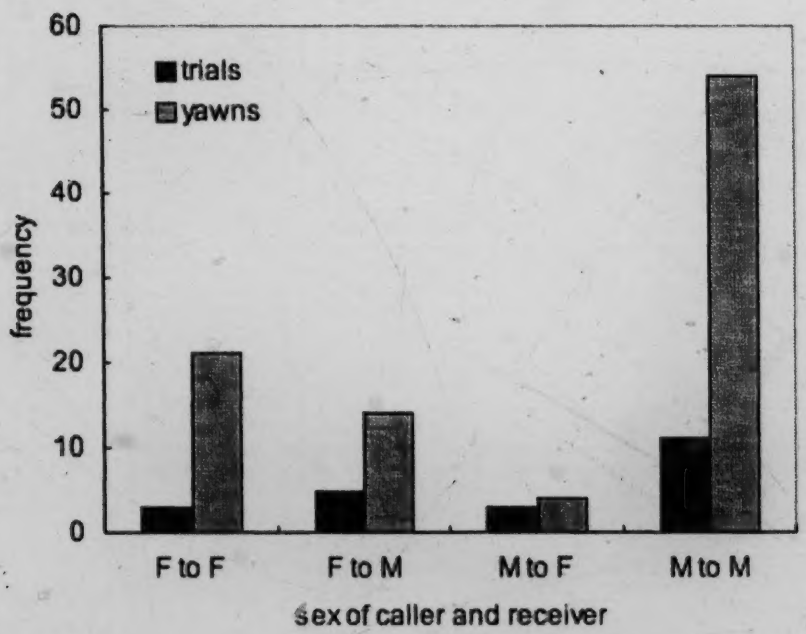

Figure 2-7. Number of trials in which "yawns" were observed and frequency of "yawns" in response to conspecific stimuli across all 3 playback experiments when sex of both caller and receiver were known. F to F denotes female stimulus played back to a female receiver, F to M=female to male, etc.

REFERENCES

Aubin, T., P. Jouventin, & C. Hildebrand. 2000. Penguins use the two-voice system to recognize each other. Proceedings of the Royal Society of London, Series B **267**:1081-1087.

Banfield, A.W.F. 1974. *The Mammals of Canada. Toronto*, University of Toronto Press, p. 120.

Bee, M.A. & H.C. Gerhardt. 2001. Neighbour-stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis. *Animal Behaviour* **62:**1129-1140.

Bee, M.A. & H.C. Gerhardt. 2002. Individual voice recognition in a territorial frog (*Rana catesbeiana*). Proceedings of the Royal Society of London Series B **269**:1443-1448.

Beever, E.A., P.F. Brussard & J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy **84**: 37-54.

Blumstein, D.T. 1995. Golden-marmot alarm calls. I. The production of situationally specific vocalizations. Ethology **100**:113-125.

Blumstein D.T. & K.B. Armitage. 1997. Alarm calling in yellow-bellied marmots, I: the meaning of situationally variable alarm calls. Animal Behavior **53**:143–171.

Blumstein, D.T. & W. Arnold. 1995. Situational specificity in alpine-marmot alarm communication. Ethology **100**:1-13.

Blumstein, D.T. & J.C. Daniel. 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. Animal Behaviour **68**:1257-1265.

Blumstein, D. T., L. Verneyre, & J.C. Daniel. 2004. Reliability and the adaptive utility of discrimination among alarm callers. Proceedings of the Royal Society of London Series B **271**:1851–1857.

Bradbury, J.W., & S.L. Vehrencamp. 1998. *Principles of Animal Communication*, Sunderland, Massachusetts, Sinauer Associates, pp. 1-11, 571-615.

Cheney, D.L., & R.M. Seyfarth. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. Animal Behavior **36**:477-486.

Conner, D.A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy **63**:48-52.

Conner, D.A. 1983. Response of pikas to playback of geographic variations of the short call. Journal of Mammalogy **64**:336-337.

Conner, D.A. 1984. The role of an acoustic display in territorial maintenance in the pika. *Canadian* Journal of Zoology **62**:1906-1909.

Conner, D.A. 1985. The function of the pika short call in individual recognition. Journal of Comparative Ethology **67**:131-143.

Cresswell, W. 1994. Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviors of skylarks (*Alauda arvensis*)

on attach by merlins (*Falco columbarius*). Behavioral Ecology and Sociobiology **34**:217-223.

Daniel, J.C. & D.T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour **56**:1517-1528.

Dearing, M.D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. Oecologia **108**:467-478.

Deputte, B.L. 1994. Ethological study of yawning in primates: I. Quantitative analysis and study of causation in two species of Old World monkeys (*Cercocebus albigena* and *Macaca fascicularis*). Ethology **98**:221-245.

Evans, C.S. 1997. Referential signals. Perspectives in Ethology **12**:99-143.

Fichtel, C. 2004. Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. Animal Cognition **7**:45-52.

Frank, D.; M. Minero, S. Cannas, & C. Palestrini. 2007. Puppy behaviours when left home alone: A pilot study. Applied Animal Behaviour Science **104**:61-70.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. MSc. thesis, University of Alberta.

Franken, R.J. & Hik, D.S. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology **73**:889-896.

Hardouin, L.A., P. Tabel, & V. Bretagnolle. 2006. Neighbour-stranger discrimination in the little owl, *Athene noctua*. Animal Behaviour **72**:105-112.

Hare, J.F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. Animal Behaviour **55**:451-460.

Hare, J.F., & B.A. Atkins. 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behavioral Ecology and Sociobiology **51**:108-112.

Harvey, E.B., & L.E. Rosenberg. 1960. An apocrine gland complex of the pika. Journal of Mammalogy **41**:213-219.

Hasson, O. 1991. Pursuit-deterrent signals—communication between prey and predator. Trends in Ecology and Evolution **6**:325-329.

Hayes, A.R. & N.J. Huntly. 2005. Effects of wind on the behaviour and call transmission of pikas (*Ochotona princeps*). Journal of Mammalogy **86**:974-981.

Holmes, W.G. & S.J. Dirks. 1978. Daily song patterns in golden-crowned sparrows at 62°N latitude. Condor **80**:92-94.

Ivins, B.L. & A.T. Smith. 1983. Responses of pikas (*Ochotona princpes*, Lagomorpha) to naturally occurring terrestrial predators. Behavioral Ecology and Sociobiology **13**:277-285.

Jaeger, R.G. 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist **117**:962-974.

Jouventin, P., T. Aubin & T. Lengagne. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. Animal Behaviour **57**:1175-1183.

Kroodsma, D.E., B.E. Byers, E. Goodale, S. Johnson, & W. Liu. 2001. Pseudoreplication in playback experiments, revisited a decade later. Animal Behaviour **61**:1029-1033.

Leger, D.W. 1993. Contextual sources of information and responses to animal communication signals. Psychological Bulletin **113**:295-304.

MacDonald, S. & C. Jones. 1987. *Ochotona collaris*. Mammalian Species no. 281. The American Society of Mammalogists, pp. 1-4.

Maynard Smith, J. 1965. The evolution of alarm calls. American Naturalist **94**:59-63.

McGregor, P.K., & T. Dabelsteen. 1996. Communication Networks. In: *Ecology and Evolution of Acoustic Communication in Birds*. Kroodsma, D.E. & E.H. Miller (eds), New York, Cornell University Press, pp. 409-425.

McKechnie, A.M., A.T. Smith, & M.M. Peacock. 1994. Kleptoparasitism in pikas (*Ochotona princeps*): theft of hay. Journal of Mammalogy **75**:88-491.

Meaney, C.A. 1983. Rate and location of scent marking by pikas during the breeding season. In: *Chemical signals in vertebrates*. Vol. 3. Muller-Schwarze, D., & A. Silverstein (eds), New York, Plenum Press, pp 329-332.

Meaney, C.A. 1986. Scent-marking in pikas (*Ochotona princeps*): test of a breeding-facilitation hypothesis. In: *Chemical signals in vertebrates*. Vol. 4. Duvall, D., D. Müller-Schwarze, & R. M. Silverstein (eds), New York, Plenum Press, pp. 571-577.

Melchior, H.R. 1971. Characteristics of Arctic ground squirrel alarm calls. Oecologia **7**:184-190.

Melman, D.S., & W.A. Searcy. 1999. Microgeographic song discrimination in a nonterritorial passerine, the boat-tailed grackle. The Condor **101**:845-848.

Möller, A.P. 1992. Interspecific response to playback of bird song. Ethology **90**:315-320.

Morrison, S.F. & D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology **76**:899-907.

Nuechterlein, G.L. 1981. Information parasitism in mixed colonies of western grebes and forster terns. Animal Behaviour **29**:985-989.

Peake, T.M., G. Matessi, P.K. McGregor, & T. Dabelsteen. 2005. Song type matching, song type switching and eavesdropping in male great tits. Animal Behaviour **69**:1063-1068.

Rainey, H.J., K. Zuberbühler & P.J.B. Slater. 2004. Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society of London, Series B **271**:755-759.

Seyfarth, R., & D. Cheney. 1990. The assessment by vervet monkeys of their own and another species alarm calls. Animal Behaviour **40**:754-764.

Shelley, E.L., & D.T. Blumstein. 2004. The evolution of vocal alarm communication in rodents. Behavioral Ecology **16**:169-177.

Shriner, W.M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour **55**:529-536.

Smith, A.T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology **55**:1368-1376.

Smith, A.T. 1981. Population dynamics of pikas. In: *Proceedings of the World Lagomorph Conference*. Myers, K. & C.D. MacInnes (eds), Guelph, Ontario, Guelph University Press, pp. 325-329.

Smith, A.T., & B.L. Ivins. 1984. Spatial relationships and social organization in adult pikas: A facultatively monogamous mammal. Journal of Comparative Ethology **66**:289-308.

Smith, W.J. 1965. Message, meaning and context in ethology. American Naturalist **99**:405-409.

Smith, W.J. 1977. *The behaviour of communicating: an ethological approach*. Cambridge, Massachusetts, Harvard University Press.

Somers, P. 1973. Dialects in southern Rocky Mountain pikas, *Ochotona princeps* (Lagomorpha). Animal Behaviour **21**:124-137.

Stoddard, P.K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and evolution of acoustic communication in birds*. Kroodsma, D.E. & E.H. Miller (eds), New York: Cornell University Press, pp. 356-374.

Temeles, E.J. 1994. The role of neighbours in territorial systems: when are they 'dear enemies'? Animal Behaviour **47**:339-350.

Templeton, C.N. & E. Greene. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America* **104**:5479-5482.

Weiss, D. J. & M.D. Hauser. 2002. Perception of harmonics in the combination long call of cottontop tamarins, *Saguinus Oedipus*. Animal Behaviour **64**:415-426.

Wilson, D.R. & J.F. Hare. 2004. Ground squirrel uses ultrasonic alarms. Nature **430**:523.

Ydenberg, R.C., L.A. Giraldeau, & J.B. Falls. 1988. Neighbors, strangers, and the asymmetric war of attrition. Animal Behaviour **36**:343-347.

Zuberbühler, K., D. Jenny, & R. Bshary. 1999. The predator deterrence function of primate alarm calls. Ethology **105**:477-490.

Chapter 3: Variation in collared pika (*Ochotona collaris*) vocalizations within and between populations

INTRODUCTION

Animal communication is characterized by considerable vocal variation within and between populations (Naguib et al. 2001). Variation in call frequency and duration is well-documented in birds (e.g. Hunter & Krebs 1979, Ballentine 2006, Förschler & Kalko 2007, Podos 2007) and has also been explored in mammals (e.g. seals: Collins & Terhune 2007, Risch et al. 2007; dolphins: Ansmann et al. 2007; orangutans: Delgado 2007). Geographic variation may reflect genetic, behavioural, and ecological differences, and therefore has implications for resolving evolutionary and behavioural questions. Studying call variation may reveal information about life history trends, the influence of genetics on signal structure, and patterns of dispersal and migration (see reviews in Mundinger 1982, Lynch 1996, Martens 1996).

Macrogeographic variation in animal vocalization is often attributed to genetic differences caused by geographic isolation or stochastic processes such as genetic drift. Many other factors may play a role, including anatomical differences, sexual selection, vocal learning, and adaptation to local environments (e.g. Asnann et al. 2007, Collins & Terhune 2007, Delgado 2007, Risch et al. 2007). Our understanding of the mechanisms driving geographic call variation in mammals remains incomplete.

One of the leading theories used to explain geographic call variation in animals is adaptation to local acoustic environments. As sound is transmitted across the landscape, calls attenuate (experience amplitude loss), degrade (change acoustic structure), and compete with background noise (Wiley & Richards 1978, 1982; Dusenbery 1992; Endler 1992; Forrest 1994) to varying degrees, depending on the structure of the habitat. The acoustic adaptation hypothesis (AAH) assumes that structural differences between habitats will influence sound transmission, and predicts that certain types of vocalizations will transmit with less overall degradation than others in a given environment (Morton 1975). The AAH suggests that selection should act on call parameters to achieve the greatest possible transmission through local habitats (Daniel & Blumstein 1998). Selection pressures imposed by the acoustic environment may therefore be a factor influencing call variation across populations. An increasing body of evidence suggests that environmental adaptation has been important in driving the evolution of song characteristics in birds.

Structural differences in bird songs from different habitat types are consistent with predictions made based on the acoustic adaptation hypothesis (Hunter & Krebs 1979; Blumstein & Turner 2005; Seddon 2005; Baker 2006; Nicholls & Goldizen 2006; Tubaro & Lijtmaer 2006). In a meta-analysis that tested the evidence for the AAH in birds, Boncoraglio and Saino (2007) found that predictions of the hypothesis were supported for all frequency variables, but

not for the single temporal variable (interval duration between notes or syllables). The effect size of habitat structure on song frequency variables ranged from low to medium. However, other factors such as eavesdropping by predators and parasites and the energetic costs of signal production may also influence the evolution of bird song (Boncoraglio & Saino 2007).

Few studies have tested the acoustic adaptation hypothesis in mammals. Habitat structure was proposed as one factor that may have contributed to alarm call differences between colonies of Gunnison's prairie dogs (*Cynomys gunnisoni*, Perla & Slobokchikoff 2002) and 'coo' call differences between two populations of Japanese macaques (*Macaca fuscata yakui*, Sugiura et al. 2006). Daniel and Blumstein (1998) did not find support for the AAH in the alarm calls of four marmot species, though there were differences in the transmission properties of calls through various habitats. One of my objectives was to test specific predictions of the AAH in another vocal mammal species, the collared pika (*Ochotona collaris*).

Call variation also occurs on an individual level. Individually unique vocalizations have been documented in at least 136 species of birds (Stoddard 1996), in amphibians (Bee & Gerhardt 2002), and in many mammals, including Richardson's ground squirrels (*Spermophilus richardsonii*, Hare 1998), greater spear-nosed bats (*Phyllostomus hastatus*, Boughman & Wilkinson 1998), African wild dogs (*Lycaon pictus*, Hartwig 2005), white-nosed

coatis (*Nasua narica*, Maurello et al. 2000), yellow-bellied marmots (*Marmota flaviventris*, Blumstein et al. 2004), and American pikas (*Ochotona princeps*, Conner 1985a). The function(s) of individually distinct calls is difficult to determine (Blumstein & Munos 2005). Individual variation, combined with the ability to detect these differences, can lead to individual discrimination (Stoddard 1996). The ability to discriminate between individuals may be driven by factors such as the cost of aggressive encounters (Hardouin et al. 2006), by differences in caller reliability (Cheney & Seyfarth 1988, Hare & Atkins 2001, Blumstein et al. 2004), or by the advantages of assessing kinship (Hare 1998, Hare & Atkins 2001). Many animals are able to distinguish between neighbours and strangers acoustically (e.g. Frommolt et al. 2003, Radford 2005, Hardouin et al. 2006), and species often react more aggressively to territorial intrusions by non-neighbours versus neighbours. By being tolerant of established neighbours that are acoustically identifiable, the energy expended on aggressive acts and the frequency of escalated contests can be minimized (Ydenberg et al. 1988). This has been termed the 'dear enemy' phenomenon (Fisher 1954, Jaeger 1981).

Study Organism

Collared pikas are small (~160 g), non-hibernating, food-hoarding lagomorphs inhabiting alpine boulderfields in Yukon, Alaska, Northwest Territories, and northern British Columbia (Smith 1981, MacDonald & Jones 1987). They are territorial and facultatively monogamous, and inhabit spatially isolated patches

of talus separated by alpine meadows (Smith & Ivins 1984, Franken & Hik 2004). Pikas provide an excellent opportunity to study questions about animal communication. In the summer months when they are making food caches for the winter ("haying"), they are easily observed, call frequently and repeatedly, are territorial and therefore easy to locate, and easily habituate to human presence (Smith 1974, Conner 1983, Dearing 1996, Beever et al. 2003).

Very little is known about the vocalizations of collared pikas. However, research on the calls of the related American pika (*O. princeps*) indicates that the function of calls is two-fold, serving as a predator alarm and in territory defense (Somers 1973, Conner 1982, Ivins & Smith 1983, Conner 1985, Hayes & Huntly 2005). American pikas are the only other North American pika, and share many life history traits with collared pikas (Franken 2002). Their vocal repertoire appears to be more extensive than that of collared pikas, though the American pika "short call" most closely resembles the vocalizations of collared pikas in form and function (Conner 1985b). In many organisms, vocalizations are critical to maintain and define social relationships (e.g. Esser 1994, Insley 2000, Robbins 2000), and pika vocalizations are likely important factors in maintaining social organization (Conner 1985b). The vocalizations of American pikas are distinct enough to allow individual recognition and show geographic variation (Conner 1982, 1985b). Individual recognition may be important to collared pikas, particularly in social interactions involving movement through conspecifics' territories during foraging, when searching for

mates during the breeding season, in direct aggression and altruism behaviour such as alarm calling, and when making dispersal and settlement decisions (Conner 1985b, Franken 2002). American pikas are able to discriminate between individual callers by sound alone (Conner 1985a), and I predicted that the energetic benefits associated with individual discrimination would have driven individual differences in call structure between collared pikas.

Objectives

In this chapter, I examine geographic call variation in collared pikas living in Yukon and Alaska to determine whether populations have distinct 'dialects' and if so, which call characteristics are responsible for population differentiation. I incorporated a species-level comparison between collared and American pika calls from Alberta, in order to determine the extent and causes of the audible vocal variation between the two North American species. Understanding the sources of vocal variation will lead to a better understanding of the mechanisms leading to variability in animal communication.

I also tested the acoustic adaptation hypothesis as a driving factor influencing interspecific call variation, by playing back and re-recording American and collared pika vocalizations in their own and their relative's habitat. While genetic divergence is perhaps the simplest explanation of vocal differences between pika populations, support for acoustic adaptation to local

environments in other species warrants testing the AAH in pikas. If calls have adapted to their local habitat, I predicted that local calls would transmit with less overall degradation than foreign calls when played back in a particular location. A species-level comparison of call transmission across habitats was particularly relevant given the audible differences in call structure between collared and American pikas.

Finally, I tested the variation in pika call structure at an individual level, by calculating the potential for individual coding (PIC) of calls. In Chapter 2 (Experiment 3), I demonstrated that collared pikas are able to discriminate between individual callers. Calculating PIC values allowed me to identify the call characteristics that have the potential to carry information regarding individual identity.

METHODS

Geographic call variation

Collared pikas were recorded at several sites in Yukon and Alaska from 18 June to 17 August, 2006 and 23 June to 4 August, 2007, and American pikas were recorded at several locations in Jasper National Park, Alberta from 27 to 29 August, 2006 and from 23 to 24 June, 2007 (Table 3-1, Fig. 3-1). Pikas were recorded using a Marantz Professional Solid State digital recorder (Model PMD671) and non-directional microphone (Model AT835b, Altec Lansing, Broadcast & Production Microphones, frequency response 40 to

20000 Hz). Calls were digitized at a sample rate of 44,100 Hz (16-bit samples/s) and analyzed as spectrograms (bandwidth 0-20,000 Hz) and power spectra using SIGNAL 4.0 (Engineering Design 2003, Belmont, MA, USA).

Twenty-one acoustic features were measured (Table 3-2). To standardize the analyses, each individual call was saved as a separate file with a duration of 1000 ms. Frequency measurements (in kHz) and were taken from a digital spectrogram with a fast Fourier Transform (FFT) window size of 1024 points and a frequency precision of 43 Hz (Fig. 3-2A). Duration measurements (in ms) were taken on a digital spectrogram with a FFT window size of 256 points and a temporal precision of 5.8 ms (Fig. 3-2B). All spectrogram measurements were performed using a cutoff amplitude of -60 dB relative to the peak amplitude of the call. I also measured the loudest frequency (FMAX) using a power spectrum (smoothing width=88.2 Hz, frequency precision=0.7 Hz; Fig. 3-2C).

I investigated geographic call variation using classification trees in R 2.4.1 (R foundation for Statistical Computing, 2006, http://www.R-project.org) using the RPART library (Therneau & Atkinson 2006). The theory of classification trees is well described in Breiman et al. (1984) and Faraway (2006). Briefly, classification trees are a regression technique used to separate multivariate data into increasingly homogeneous groups of predominantly one class

through recursive partitioning. Classification trees implicitly include interactions among predictor variables and allow the use of categorical and continuous data, non-linear relationships, and missing values (Karels et al. 2004, Faraway 2006). Each split is binary, and is based on a threshold value of the predictor variable that produces the greatest within-group similarity for the response variable. To determine which predictor variable at what value is chosen to perform the next split, the maximum reduction in deviation over all splits is calculated (see chapter 10 in Venables & Ripley 1999). To achieve the optimal tree size and avoid overfitting of variables, pruning is used. I used a 10-fold crossvalidation pruning procedure described by Faraway (2006). Classification trees are graphically represented with the root node on top and terminal nodes (leaves) below. The deviance explained by each node is proportional to its depth. Classification trees have been successfully used to describe geographic vocal variation in previous mammal studies (Van Parijs et al. 2003, Risch et al. 2007).

For my classification tree analyses, call parameters were averaged for each individual. Because the number of pikas recorded across sites varied (from 8 to 120), call parameters were weighted by the square root of the number of individuals recorded at each location. Two classification trees were constructed; the first contained only collared pika calls, the second included calls of both collared and American pikas broken into broader geographic regions than the first.

Acoustic Adaptation

Collared (n=20) and American (n=13) pika calls recorded in 2006 and 2007 were all re-broadcast along transects running across slope in the habitats of both species at four sites in calm conditions (average wind speed 1.0 m/s). In instances where a call was broadcast through its own environment (collared pika calls played in collared pika habitat, and American pika calls played in American pika habitat), I refer to these as "resident" calls. When a call was broadcast through the other species' habitat (collared pika calls played in American pika habitat and vice-versa), I refer to these calls as "foreign". Sites of American pika habitat were in Alberta: three in Jasper and one in Lake Louise. Collared pika sites were in the Yukon and Alaska (Table 3-1). Calls were transmitted from an iPod mini (Apple Inc., Cupertino, CA, USA) through Altec Lansing iM4 speakers (Milford, Pennsylvania, frequency response 60 Hz to 20 kHz), set on a rock at the approximate height of a calling pika, and were re-recorded at 5 and 10 m using a Marantz Professional Solid State digital recorder (Model PMD671, Mahwah, NJ, USA) at a sampling rate of 44100 Hz, 16-bit sample/s, and a shotgun microphone (Model AT835b, Audio Technica, Broadcast & Production Microphones, Stow, OH, USA) that was level with and faced directly towards the speakers. Preliminary trials indicated that in some environments, calls recorded at greater distances were too severely degraded to analyze. Ten metres, however, represents a biologically meaningful distance in which pika calls could be transmitted between neighbours as they

move across talus (Broadbooks 1965, Franken 2002). Calls were re-recorded along transects that ran across the main slope.

Calls were saved as spectrograms in SIGNAL, and low frequency, high frequency, bandwidth, frequency of band 1 to 5, dominant start frequency, dominant end frequency, total duration, dominant total duration, and frequency of maximum amplitude (Table 3-2) were measured as above. For each call, the difference between each measurement recorded at 5 and 10 m was used in the analysis.

Initial data exploration revealed that data were not normally distributed and transformation did not significantly increase the normality of the dependent variables. Since the assumption of homogeneity of variance was not met, I performed one-way ANOVAs on each call parameter, and calculated Welch's and Brown-Forsythe F-values, which are robust when homogeneity of variance has been violated (Field 2005). The corrected F-values were only marginally different from the uncorrected F-values, and did not affect the significance in any case. Therefore, I performed a multivariate analysis of variance (MANOVA) to explore the differences between transmissions of pika calls across native versus foreign habitats. Two factors were explored in the MANOVA: the effect of residency (resident or foreign) and site on overall acoustic degradation, measured as the difference between call parameters recorded at 5 and 10 m. F-statistics presented are Roy's Greatest Root.

American pika sites were: 1) Maligne Lake Road, 2) Maligne River, and 3) Jonas Slide, Jasper, and 4) First Consolation Lake, Lake Louise. Collared pika sites were: 1) Denali Highway, Alaska, 2) Vulcan Mountain, 3) Pika Camp, and 4) Valley of the Five Lakes, Yukon (Table 3-2).

Potential for Individual Coding

The potential for individual identity coding (PIC) can be determined by calculating the ratio between the coefficient of variation between calls (CV_b) and the mean of the coefficients of variation within calls (mean CV_w). Calls must show a highly individual vocal signature to support individual recognition. Acoustic signals with a PIC> 1 are generally regarded as parameters that may yield information on individual identity, since they have greater inter-individual than intra-individual variability (Robisson et al. 1993; Lengagne et al. 1998; Charrier et al. 2001, 2002; Mathevon et al. 2003). I explored the PIC in the pika population at our main study site in the Ruby Range Mountains, southwestern Yukon, using the ratio of the coefficient of variation between individuals ($CV_b = (SD/X_{mean})*100$ where X_{mean} is the overall mean and SD is the standard deviation for each call parameter) and the coefficient of variation within individuals ($CV_w = (SD/ X_{mean})(1+¼n)*100$, where X_{mean} is the mean, SD is the standard deviation of the individual means, and *n* is the number of calls per individual; Sokal & Rohlf 1995; Robisson et al. 1993).

RESULTS

Geographic call variation

A total of 720 calls from 283 individuals (mean of 5.0±3.7 calls per individual) were used to test for geographic call variation. A summary of the frequency (Table 3-3) and duration (Table 3-4) parameters are given for each location. Pikas were assigned to their correct populations based on call structure 75% of the time, with terminal nodes ("leaves") varying in accuracy from 36 to 91% (Fig. 3-3). When pikas were classified into broader geographical areas, the overall tree accuracy increased to 94%, with leaves varying from 64 to 100% accuracy (Fig. 3-4), indicating that substantial differences exist in call structure between pika populations. The classification tree using fine-scale geographic areas made errors when smaller numbers of pikas were recorded from a population. In these instances, pikas were grouped with larger populations, contributing to the reduced accuracy.

The first split was driven by high frequency (HF) of calls, and placed individuals from both Alaska and Pika Camp (southwest Yukon) in separate groups. The frequency of the second band (F2) drove further splitting between Alaska and the Ruby Range populations (Pika Camp and Valley of the Five Lakes). Total duration, F2, and fundamental total duration (FTD) were the predictor variables that caused subsequent splitting between Pika Camp and the Valley of the Five Lakes.

In the classification tree incorporating calls of both pika species, proximal sites were grouped together into broader geographic categories. In this analysis, the Ruby Range sites segregated out from all other sites based on the frequency of the fifth band (F5). American pikas recorded in Jasper separated out from the collared pika sites based on total duration of the calls. Dominant start frequency (DSF) and fundamental end frequency (FEF) drove the subsequent divisions between the Front Range Sites, Tombstone, and Alaska.

Acoustic Adaptation

In the two-way MANOVA, whether pikas were resident or foreign did not affect how calls transmitted across space ($F_{13,227}$=1.467, p=0.131, Fig. 3-5). Site had a significant effect on call transmission ($F_{13, 233}$=24.696, p<0.0001, Fig. 3-6). Individual ANOVAs subsequently indicated that most parameters varied between sites: LF (F_7=40.358, p<0.0001), HF (F_7=10.905, p<0.0001), BW (F_7=10.588, p<0.0001), F1 (F_7=34.821, p<0.0001), F2 (F_7=30.381, p<0.0001), F3 (F_7=27.967, p<0.0001), F4 (F_7=24.016, p<0.0001), F5 (F_7=19.653, p<0.0001), TD (F_7=3.284, p<0.0001), and FMAX (F_7=2.901, p<0.0001). Measurements of the dominant band did not vary significantly between sites: DSF (F_7=1.300, p=0.251), DEF (F_7=0.764, p=0.618), and DTD (F_7=1.385, p=0.212). There was a significant interaction between residency and site ($F_{13,232}$=4.922, p<0.0001) in the case of LF (F_6=4.726, p<0.0001) and BW (F_6=2.199, p=0.044). The differences in these two parameters between resident and foreign calls did not follow the pattern expected by acoustic

adaptation (that is, residents did not transmit with less degradation) and it is unlikely that the interaction is biologically meaningful.

Potential for Individual Coding

I recorded an average of 8.3 calls from 120 individual pikas in 2006 and 2007 at our main study site in southwestern Yukon to explore what elements of call structure might carry information about individual identity. The PIC was > 1 for the frequencies of bands 1 through 5, but not for other call measurements (Table 3-5). Bands 4 and 5 had PIC values approaching 2. Bands at higher frequencies therefore contained enough information to allow the potential for individual recognition.

DISCUSSION

Geographic call variation

Pika vocalizations were distinct between populations and could generally be classified into their correct populations based on time and frequency measurements. The accuracy of the classification tree for predicting population origin could likely be improved by increasing the sample sizes from the smaller populations so that they are less likely to be grouped into other populations, which could be facilitated by sampling over multiple years at some sites. Geographic call variation may reflect genetic divergence, and be a result of populations with separate evolutionary histories (Sommers 1973, Conner 1982). Calls from proximal populations separated by a mountain ridge,

for example, did not have highly divergent call structure. This may reflect gene flow between populations, which would suggest that large geographic features may not be dispersal barriers for pikas. However, pika dispersal is thought to be limited by the risk of predation off-talus, and geographic variation in calls over larger distances may reflect lack of gene flow (Conner 1983). Geographic variation in call structure may increase our understanding of pika metapopulation dynamics and dispersal if it reflects genetic divergence (Conner 1983).

In the classification tree including both species, American pika calls recorded in Jasper did not separate from all other collared pika calls recorded in the Yukon and Alaska. Broadbrooks (1965) made note of greater call variation within American pikas than between American and collared pikas. The similarity in call structure between these two species may reflect a recent genetic divergence (see Grayson 2005) or vocal adaptation to similar habitats (Conner 1982).

Acoustic Adaptation

I found no evidence that acoustic adaptation was responsible for the structural differences in the vocalizations of American and collared pikas. Calls of both species transmitted similarly at 5 and 10 m, whether they were broadcast in the habitats of con- or heterospecifics. There was, however, a significant difference in call transmission between sites.

Therefore, while local environmental factors such as proximity of vegetation, boulder size, and humidity (among others) influenced call transmission between sites, the similarities between American and collared pika habitats may impose comparable environmental selection pressures on acoustic parameters. Selection pressure imposed by the acoustic environment may play a role in limiting the variability in vocalizations of animals inhabiting similar environments (Conner 1982, Daniel & Blumstein 1998).

It is possible that American and collared pikas underwent speciation recently enough that their call structures have not yet fully adapted to their respective habitats. However, it seems more likely that the acoustic environment of the two species is similar, and that the evolution of species-specific vocalizations has been driven by factors other than the acoustic environment.

Several methodological limitations should be taken into consideration, which may limit the ability of this study to detect acoustic adaptation. The first is the relatively short distances that re-broadcast calls were transmitted, due to extreme degradation over greater distances making it impossible to take certain measurements. Calls broadcast over greater distances would receive more "exposure" to the environment, and could more accurately test how calls degrade as they are transmitted through the habitat. A second consideration is whether the measurements taken represent true degradation, as pikas

perceive it. I did not measure specific parameters of degradation (reverberation, irregular amplitude fluctuations, frequency-dependent degradation; Daniel & Blumstein 1998). However, taking specific time and frequency measurements across the entire bandwidth of the call allowed me to measure parameter-specific attenuation and degradation, and was likely a good indication of perceived degradation.

While studies examining bird (Boncoraglio & Saino 2007) and mammal calls (Perla & Slobokchikoff 2002, Sugiura et al. 2006) have found support for the acoustic adaptation hypothesis, this study is not the first to fail to support it (e.g. see Date & Lemon 1993, William & Slater 1993, Fotheringham et al. 1997, Daniel & Blumstein 1998). Studies supporting the AAH have examined signal structure differences between broad habitat categories (e.g. open versus forested habitat) or for either many species or many geographic variants of one species, while studies that examined fewer species, fewer geographic variants, or finer differences between habitats have typically not supported the AAH (Daniel & Blumstein 1998).

Other factors cited as important in shaping signal structure include exposure to predators (Marler 1955, 1957), social complexity (Blumstein & Armitage 1997), and the relative distribution of signal recipients (Tubaro & Segura 1994, Fotheringham et al. 1997), but these factors are not likely to differ significantly between American and collared pikas. As with

geographic call variation between populations, species-specific vocalizations may be best explained by genetic divergence. An alternate explanation of call variation is vocal learning. Learning is not known to be a factor in the development of pika calls, so may not influence call variation between populations or species. Future work on structural differences in pika calls should explore what role, if any, vocal learning and genetic structuring play.

Potential for Individual Coding

In Chapter 2, I demonstrated that pikas were able to discriminate between individual callers. In this Chapter, I calculated the potential for individual identity coding for each call parameter by determining the ratio of within to between individual variation. This ratio was > 1 (the cutoff usually used to assign potential for individual identity coding) for frequency variables of bands one through five, and increased with higher frequency bands. Therefore, frequency elements of pika calls may be used as cues in individual discrimination between callers. Other call parameters, such as high frequency, may not differ greatly between individuals because they are limited by pika physiology, or because of technical recording ability. For example, the ability to record frequency was limited by the microphone and software used to analyze calls, which did not have ultrasonic (>20 kHz) capabilities. Time measurements did not appear to reveal information about individual identity. The potential for individual discrimination was supported by the habituation

playback experiment in Chapter 2, and by earlier work on American pikas showing that they are able to discriminate between individual callers by sound alone (Conner 1985a).

Individual discrimination abilities are likely of significant benefit when gauging the threat an individual poses, in accordance with the "dear enemy" hypothesis (Fisher 1954). Individual recognition may allow pikas to reduce the number of aggressive encounters by tolerating established residence calling from adjacent territories (Conner 1985a). This would seem to be of significant importance in years when population densities are quite high (Hardouin et al. 2006). It would also allow for significant energetic advantage if time can be allocated to haying, when pikas store vegetation critical to overwinter survival (Dearing 1997), rather than aggressive or defensive behaviours (Conner 1985a). Pikas give the same acoustic signal both to defend their territories and to warn against predators (Ivins & Smith 1983, Conner 1985a, Hayes & Huntley 2005). Individual discrimination may also be used as an important means of assessing kinship, to facilitate calling when relatives are nearby (Conner 1985a), or to determine caller reliability (Cheney & Seyfarth 1988; Hare & Atkins 2001; Blumstein et al. 2004). The ability to assess kin is necessary only if juveniles do not disperse great distances. Previous work at our main study site suggests that local residents are likely to be related as juveniles dispersed an average of 375 (males) and 350 (females) metres (Franken 2002).

In summary, collared pika calls vary between populations to an extent that they can be accurately classified to their geographic region based on acoustic characteristics. Acoustic adaptation is unlikely to play a role in driving species differences in vocalizations of collared and American pikas, given that their habitats are similar. Genetic differences may explain geographic and species-level call variation in North American pikas. Collared pika calls show individual differences in band frequency that may carry the information necessary for individual discrimination demonstrated in the habituation experiment of Chapter 2. Future studies exploring call variation should be done in conjunction with genetic analyses, to determine whether call structure can be used as a non-invasive method to gain insight into dispersal, migration, and metapopulation dynamics in pikas and other mammals.

Table 3-1. Locations and dates at which American (*O. princeps*) and collared (*O. collaris*) pika calls were recorded. Sites marked with an asterisk were also locations of playback in the acoustic adaptation experiment.

Abbreviation	Description
LF	low frequency
HF	high frequency
BW	bandwidth
F1	frequency of band 1
F2	frequency of band 2
F3	frequency of band 3
F4	frequency of band 4
F5	frequency of band 5
FEF	end frequency of fundamental (first) band
DSF	start frequency of dominant (loudest) band
DEF	end frequency of dominant (loudest) band
TD	total duration
FTD	total duration of fundamental (first) band
FAD	ascending duration of fundamental (first) band
FDD	descending duration of dominant (loudest) band
DTD	total duration of dominant (loudest) band
DAD	ascending duration of dominant (loudest) band
DDD	descending duration of dominant (loudest) band
NO_BANDS	number of bands
DOM_BAND	dominant band number
FMAX	frequency of maximum amplitude (loudest frequency)

Table 3-2. Locations and dates at which American (*O. princeps*) and collared (*O. collaris*) pika calls were recorded. Sites marked with an asterisk were also locations of playback in the acoustic adaptation experiment.

Species	Location	Site	Latitude, Longitude; Altitude (m)	Recording dates
O. princeps	Jasper	Tonquin Valley	52° 43' N, 142° 9'W; 2013 52° 44'N, 142° 8'W; 1925	27-28 Aug '06
		Edith Cavell	52° 44'N, 142° 8'W; 1924	29 Aug '06
		Maligne Lake Road*	52°48'N, 117°41'W; 1573 52°46'N, 117°41'W; 1580 52°43'N, 117°40W; 1604	23 June '07
		Beauty Creek Hostel	52°20'N, 117°20'W; 1578	24 June '07
O. collaris	Alaska	Unnamed Lake, Denali Highway*	63°04'N, 146°13'W; 1188	9-11 July '07
		Glacier Lake, Denali Highway	63°07'N, 146°14'W; 1200 63°05'N, 146°23'W; 1268	12-14 July '07
	Kluane, Yukon	Vulcan Mountain	60°56'N, 138°32'W; 1903	10-14 Aug, '06; 22-24 July '07
		St. Elias Icefields	60°32'N, 139°25'W; 1887 60°31'N, 139°26'W; 1848	24-29 June '07
		Mount Decoeli	60°49'N, 137°50'W; 1435	25 July '07
		'Pika Camp', Ruby Range*	61°12'N, 138°16'W; 1800	18 June-17 Aug '06; 29 July-22 Aug '07
		'East of East Lake', Ruby Range	61°13'N, 138°11'W; 1548	10 Aug '06, 4 Aug '07
		'Valley of the 5 Lakes', Ruby Range*	61°15'N, 138°11'W; 1507	1-3 Aug '07
	Tombstone Territorial Park, Yukon	Ogilvie Mountains, Dempster Highway	6°28'N, 139°47'W; 1461	13-14 July '06

Note: site names in single quotes are not official

Table 3-3. Frequency measurements taken from calls of collared (*Ochotona collaris*) and American (*O. princeps*) pikas. LF=low frequency, HF=high frequency, BW=bandwidth, F1-F5=frequency of bands 1-5, FEF=fundamental end frequency,

location mean SD	n	LF	HF	BW	F1	F2	F3	F4	F5	FEF	DSF	DEF
Alaska	31	713.18	15631.00	14913.61	1078.96	2117.25	3134.69	4165.81	5187.32	502.12	2544.23	1950.98
		81.47	2091.35	2122.10	84.15	150.80	232.42	298.33	377.04	141.22	701.28	761.33
Decoeli	9	951.19	15874.63	14915.82	1495.94	3008.81	4533.01	6026.51	7578.68	1212.76	2003.09	2608.34
		119.48	2123.64	2164.24	256.67	419.36	592.39	786.92	968.22	248.29	493.10	964.50
EEL	18	879.67	17321.68	16430.13	1469.12	2905.01	4333.79	5719.83	7095.07	1242.84	2015.99	2778.27
		88.22	1766.67	1808.10	152.75	297.01	444.38	523.72	633.14	223.92	526.06	612.49
Icefields	9	703.77	15885.47	15183.47	1040.68	2041.01	3022.99	4013.52	5001.13	520.00	4356.69	3797.99
		64.34	1169.15	1151.33	78.06	159.44	238.01	316.92	395.93	99.02	858.92	490.44
Pika Camp	121	1000.59	13577.07	12578.74	1549.55	3086.34	4603.29	6103.64	7586.61	1381.75	2156.31	3015.51
		200.78	2278.60	2318.54	189.90	340.63	518.18	698.50	887.41	300.48	498.43	852.18
Tombstone	9	801.91	11495.24	10693.32	1024.93	1877.08	2761.65	3680.74	4555.17	800.15	2425.50	2263.89
		46.22	672.30	701.77	47.47	252.90	461.40	626.98	825.05	74.85	610.55	698.76
VFL	53	946.03	17108.32	16156.02	1626.24	3229.16	4795.54	6373.99	7944.19	1368.49	2124.65	3096.28
		128.60	1639.90	1675.11	170.25	320.46	463.83	605.04	749.81	273.53	600.86	766.83
Vulcan	10	880.78	15463.62	14582.18	1532.27	2978.49	4380.41	5837.16	7227.87	1293.15	2271.24	3126.83
		165.53	2300.99	2271.33	268.75	564.14	870.61	1142.98	1515.54	247.06	607.53	613.10
Jasper*	23	727.63	16452.91	15848.82	861.55	1677.18	2485.15	3311.42	4124.92	685.98	3375.16	3474.56
		610.26	2195.01	2183.24	106.10	212.21	321.09	439.74	542.28	248.45	603.93	611.16

DSF=dominant start frequency, DEF=dominandt end frequency.

* *Ochotona princeps*, all other locations are *Ochotona collaris*

Table 3-4. Time measurements taken from calls of collared (*Ochotona collaris*) and American (*O. princeps*) pikas. TD=total duration, FTD=fundamental total duration, FAD=fundamental ascending duration, FDD=fundamental descending duration, DAD=dominant ascending duration, DDD=dominant descending duration, # bands=number of bands, dom band=number of the dominant band, Fmax=frequency of maximum amplitude.

location mean SD	n	TD	FTD	FAD	FDD	DTD	DAD	DDD	# bands	dom band	Fmax
Alaska	31	143.32	119.01	41.89	88.36	137.51	48.64	106.34	12.20	3.48	3541.44
		89.45	91.58	81.35	96.29	96.63	81.54	99.48	2.19	0.91	907.27
Decoeli	9	93.79	83.83	52.67	28.86	89.91	57.47	32.47	9.94	2.21	3264.51
		16.18	12.02	10.31	9.37	16.34	8.20	15.45	1.39	0.36	975.84
EEL	18	135.15	126.89	90.48	59.48	131.32	98.01	59.24	11.84	2.24	3049.91
		102.24	103.15	106.24	119.93	102.71	105.19	120.85	1.50	0.56	527.71
Icefields	9	142.93	121.81	33.84	88.40	116.81	37.03	80.98	14.37	5.79	5524.56
		20.13	22.66	14.70	25.09	21.52	13.28	23.04	2.02	1.39	921.18
Pika Camp	121	117.92	107.73	72.19	42.00	113.35	81.99	43.95	9.58	2.27	3210.93
		50.94	56.78	55.74	62.17	55.40	89.19	62.22	1.52	0.57	674.69
Tombstone	9	95.41	64.18	21.12	33.41	85.29	31.87	47.47	12.00	3.50	3166.69
		18.96	7.62	6.56	13.10	19.67	14.07	26.81	2.77	0.54	825.03
VFL	53	105.61	101.34	64.06	34.81	99.71	63.80	35.10	10.29	2.22	3275.99
		20.70	20.31	13.65	15.80	19.53	14.37	16.46	1.74	0.42	768.13
Vulcan	10	132.12	124.19	74.73	58.91	129.35	73.51	65.86	10.19	2.63	3497.70
		32.44	40.77	45.28	35.09	30.79	40.48	33.37	1.53	0.87	660.17
Jasper*	23	311.28	282.41	97.41	35.32	293.88	187.10	55.07	19.96	5.32	4247.89
		63.13	59.17	112.94	26.93	59.30	105.28	28.09	3.23	0.72	542.78

* *Ochotona princeps*, all other locations are *Ochotona collaris*

Table 3-5. Potential for individual coding (PIC), measured from 120 pikas (average 8.3 calls per individual) recorded at Pika Camp, Ruby Range, southwest Yukon. PIC is calculated as the ratio between the coefficient of variation between calls (CV_b) and the mean of the coefficients of variation within calls (mean CV_w). $CV_b = (SD/X_{mean})*100$ where X_{mean} is the overall mean and SD is the standard deviation for each call parameter. $CV_w = (SD/ X_{mean})(1+¼n)*100$, where X_{mean} is the mean, SD is the standard deviation of the individual means, and *n* is the number of exemplars per individual. LF=low frequency, HF=high frequency, BW=bandwidth, F1-F5=frequency of bands 1-5, FEF=fundamental end frequency, DSF=dominant start frequency, DEF=dominant end frequency, TD=total duration, FTD=fundamental total duration, FAD=fundamental ascending duration, FDD=fundamental descending duration, DTD=dominant total duration, DAD=dominant ascending duration, DDD=dominant descending duration, # bands=number of bands, dom band=number of dominant band, FMAX=frequency of maximum amplitude.

	LF	HF	BW	F1	F2	F3	F4	F5	FEF	DSF	DEF
mean	1011.11	12585.64	11574.53	1524.20	3066.70	4588.08	6083.52	7572.98	1389.14	2234.15	3123.90
SD	139.30	158.52	1604.01	210.71	373.44	559.44	734.62	936.52	250.24	685.14	1175.06
CV_b	13.78	1.26	13.86	13.82	12.18	12.19	12.08	12.37	18.01	30.67	37.62
mean CV_w	20.20	21.26	23.49	10.15	9.36	9.01	7.27	7.03	21.36	48.50	48.62
PIC	**0.68**	**0.06**	**0.59**	**1.36**	**1.30**	**1.35**	**1.65**	**1.76**	**0.84**	**0.63**	**0.77**

	TD	FTD	FAD	FDD	DTD	DAD	DDD	# bands	dom band	FMAX
mean	110.27	94.21	61.01	32.28	102.65	64.59	34.57	9.23	2.29	3265.54
SD	19.34	22.66	45.85	22.05	16.74	16.11	15.95	1.48	0.71	1019.9
CV_b	17.54	24.05	75.15	68.31	16.31	24.94	46.13	16.04	30.95	31.23
mean CV_w	26.31	34.44	79.16	109.81	25.53	40.39	80.24	22.77	39.75	45.83
PIC	**0.67**	**0.70**	**0.95**	**0.62**	**0.64**	**0.62**	**0.57**	**0.70**	**0.78**	**0.68**

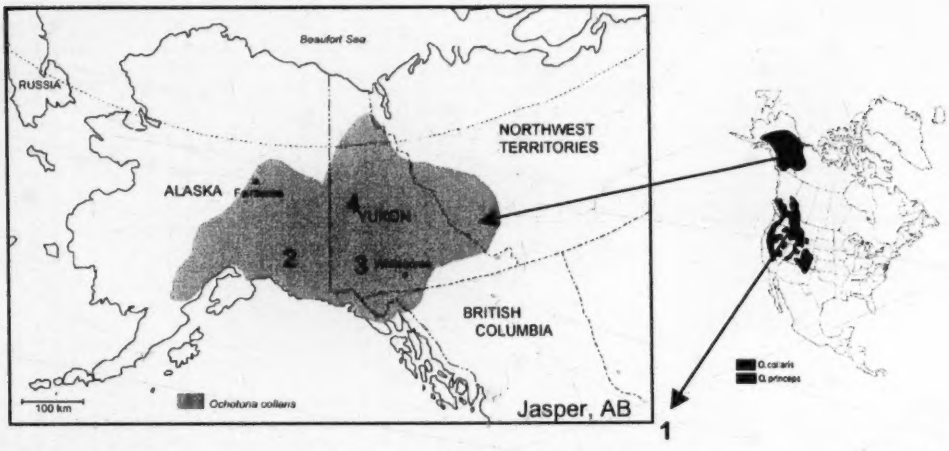

Figure 3-1. Locations at which American pikas (*Ochotona princeps*, Site 1) and collared pikas (*O. collaris*, Sites 2-4) were recorded in Alberta, Alaska, and Yukon. Map © H. Lanier.

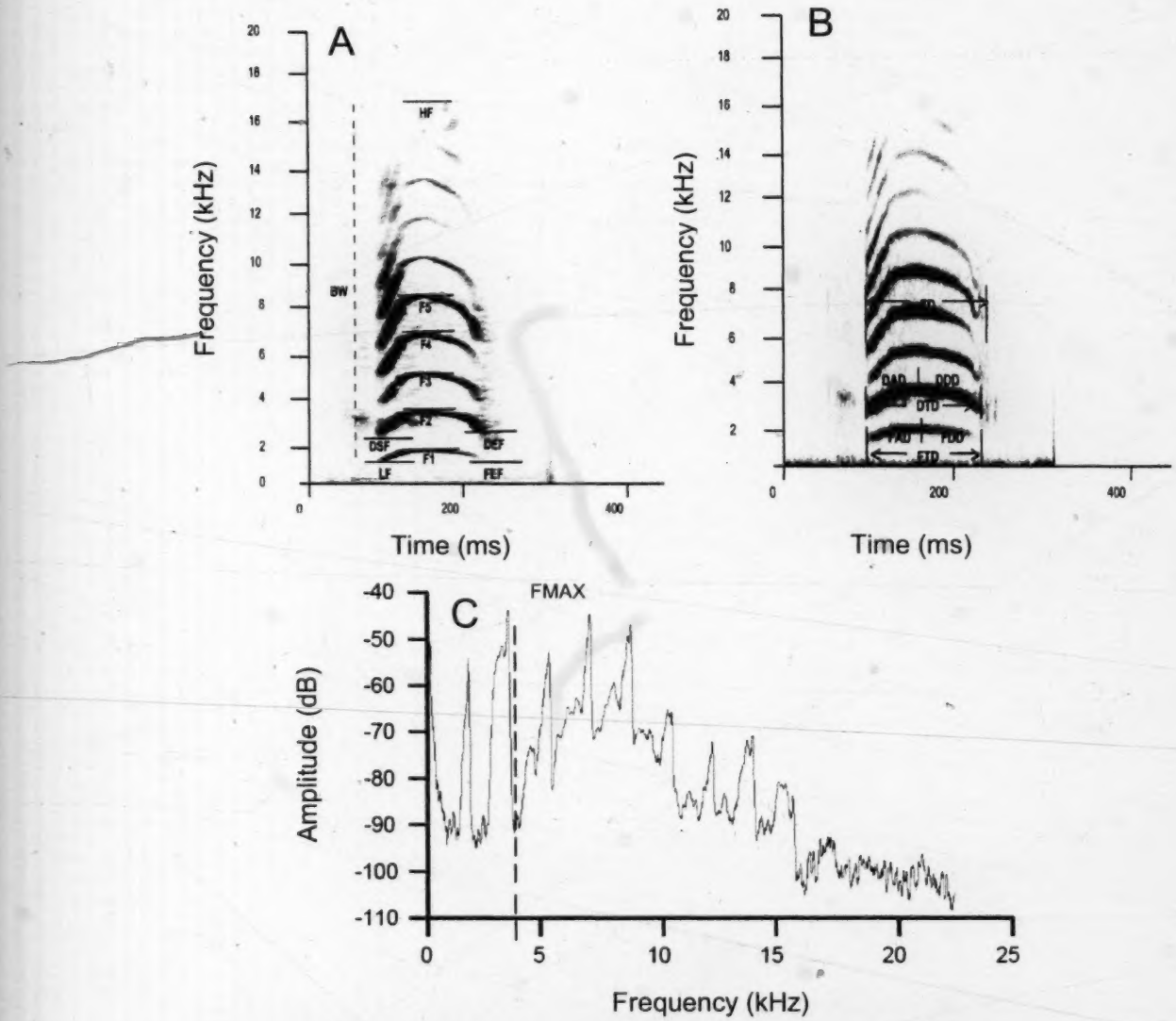

Figure 3-2. Sound spectrograms and spectrum illustrating call measurements taken on pika calls. (**A**) Sound spectrogram (FFT window=1024 points) of a representative collared pika call from Pika Camp. Vertical lines indicate approximate boundaries for low frequency (LF), high frequency (HF), the difference between these is bandwidth (BW), frequency of bands 1-5 (F1-F5), fundamental end frequency (FEF), dominant start frequency (DSF), and dominant end frequency (DEF). (**B**) Sound spectrogram (FFT window=256 points) of the same pika call from (A). Vertical lines indicate approximate boundaries for total duration (TD), fundamental band measurements: total duration (FTD), ascending duration (FAD), and descending duration (FDD), and dominant band measurements: total duration (DTD), ascending duration (DAD), and descending duration (DDD). (**C**) Sound spectrum (window size=6159 points) of a collared pika call. The vertical line illustrates the frequency of

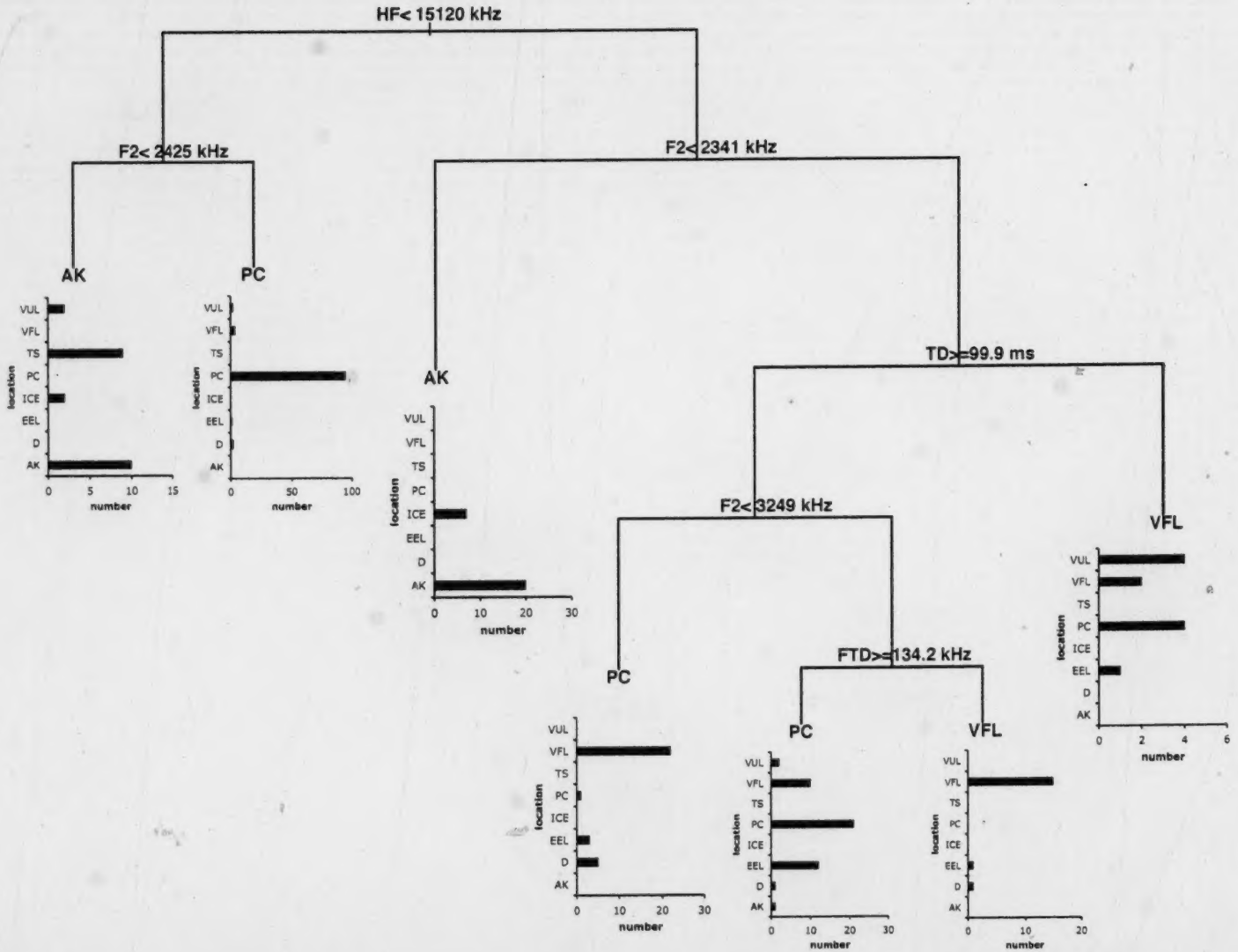
HF< 15120 kHz
F2< 2425 kHz
F2< 2341 kHz
AK
PC
AK
TD>=99.9 ms
F2< 3249 kHz
VFL
PC
FTD>=134.2 kHz
PC
VFL
VUL
VFL
TS
PC
ICE
EEL
D
AK
location
number

Figure 3-3. Classification tree to predict population origin of collared pika (*Ochotona collaris*) vocalizations based on call characteristics. Vertical line length is proportional to the amount of deviance explained by the preceding node. Summary bar graphs indicate the number of animals from each population in each node. AK=Alaska, PC=Pika Camp, VFL=Valley of the Five Lakes. Overall tree accuracy 75%.

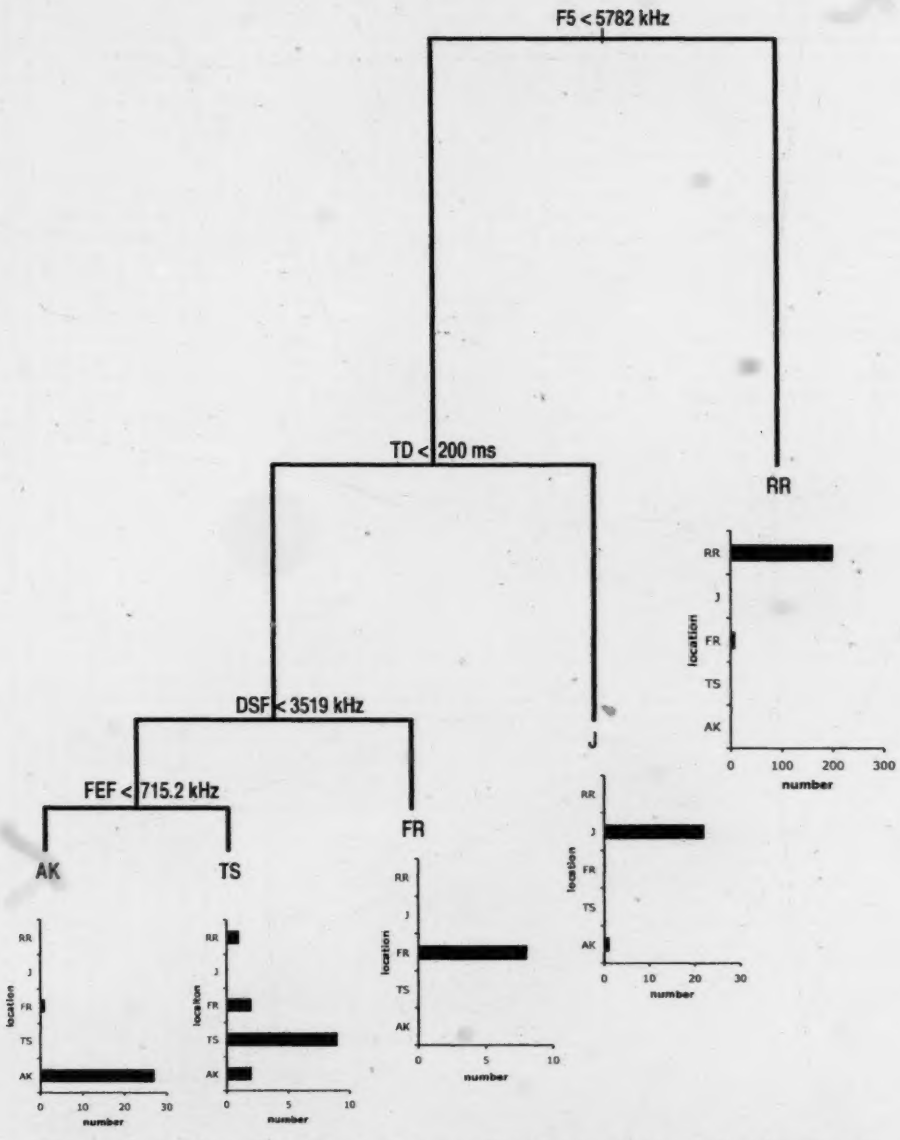

Figure 3-4. Classification tree to predict geographic origin of collared (*Ochotona collaris*) and American (*O. princeps*) pika vocalizations based on call characteristics. Vertical length is proportional to the amount of deviance explained by the preceding node. Bar graphs indicate the number of animals from each population in each node. AK=Alaska, TS=Tombstone Territorial Park, FR=Front Range, Yukon, J=Jasper, Alberta, RR=Ruby Range, Yukon. Overall tree accuracy 94%.

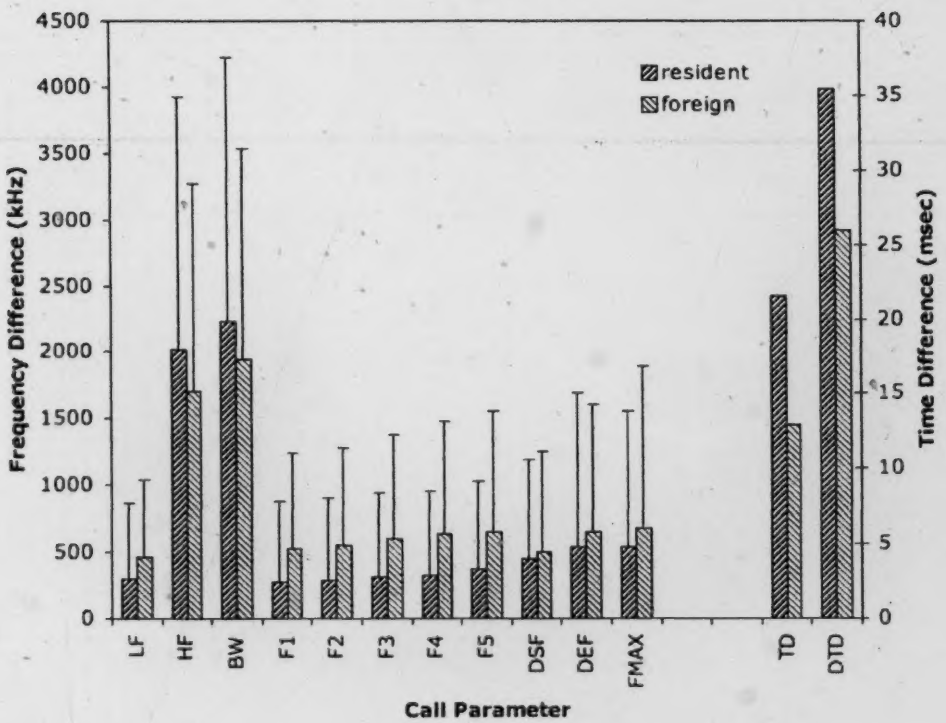

Figure 3-5. Difference between collared (*Ochotona collaris*) and American (*O. princeps*) pika call frequency measurements recorded at 10m and 5m. "Residents" were calls played back in the habitat of the same species, "foreign" pika calls were broadcast through the other species' habitat. Bars are standard deviation, and for the time values standard deviations were 61.7, 95.2; 20.7, 67.6 (TD residents, non-residents; DTD residents, non-residents, respectively). LF=low frequency, HF=high frequency, BW=bandwidth, F1-F5=frequency of bands 1-5, DSF=dominant start frequency, DEF=dominant end frequency, FMAX=frequency of maximum amplitude, TD=total duration, DTD=dominant total duration.

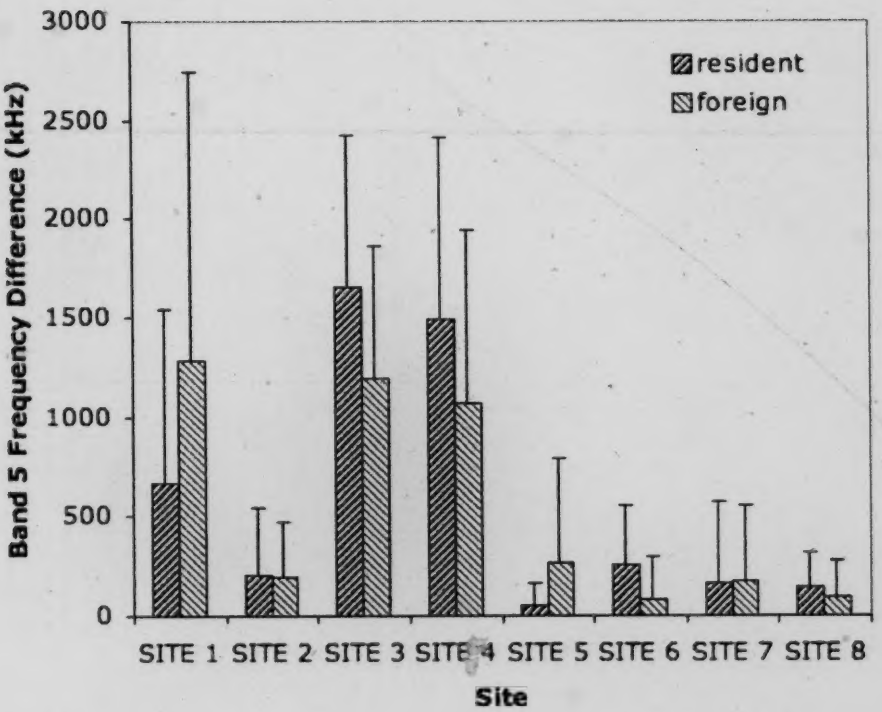

Figure 3-6. Example of how the difference in one call parameter, the frequency of band 5, broadcast and re-recorded at 10 m and 5 m varied between "resident" (species *a* broadcast in habitat of species *a*) and "foreign" (species *a* broadcast in habitat of species *b*) American (*Ochotona princeps*) and collared (*O. collaris*) pika calls differed between the eight playback sites in Alberta, Yukon, and Alaska.

REFERENCES

Ansmann, I.C., J.C. Goold, P.G.H. Evans, M. Simmonds, & S.G. Keith. 2007. Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. Journal of the Marine Biological Association of the United Kingdom **87**:19-26.

Baker, M.C. 2006. Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection on songs. Ethology **112**:757-771.

Ballentine, B. 2006. Morphological adaptation influences the evolution of a mating signal. Evolution **60**:1936-1944.

Bee, M.A., & H.C. Gerhardt. 2002. Individual voice recognition in a territorial frog (*Rana catesbeiana*). Proceedings of the Royal Society of London B **269**:1443-1448.

Beever, E.A., P.F. Brussard, & J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy **84**:37-54.

Blumstein, D. T. & K.B. Armitage, 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. American Naturalist, **150**:179–200.

Blumstein, D.T., & A.C. Turner. 2005. Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? Acta Ethologica **15**:35-44.

Blumstein, D.T., & O. Munos. 2005. Individual, age and sex-specific information is contained in yellow-bellied marmot alarm calls. Animal Behaviour **69**:353-361.

Blumstein, D.T., L. Verneyre, & J.C. Daniel. 2004. Reliability and the adaptive utility of discrimination among alarm callers. Proceedings of the Royal Society of London B **271**:1851-1857.

Boncoraglio, G., & N. Saino. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology **21**:134-142.

Boughman, J.W., & Wilkinson, G.S. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. Animal Behaviour **55**:1717-1732.

Breiman, L., J.H. Friedman, R.A. Olshen, & C. Stone. 1984. *Classification and Regression Trees*. Boca Raton, FL, Chapman & Hall.

Broadbooks, H.E. 1965. Ecology and the distribution of the pikas of Washington and Alaska. American Midland Naturalist **73**:299-335.

Charrier, I., P. Jouventin, N. Mathevon, & T. Aubin. 2001. Potentiality of individual identity coding depends on call type in the South Polar Skua *Catharacta mccormicki*. Polar Biology **24**:378-382.

Charrier, I., N. Mathevon, & P. Jouventin. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. Journal of Experimental Biology **205**:603-612.

Cheney, D.L., & R.M. Seyfarth. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. Animal Behaviour **36**:477-486.

Collins, K.T., & J.M. Terhune. 2007. Geographic variation of Weddell seal (*Leptonychotes weddellii*) airborne mother-pup vocalizations. Polar Biology **30**:1373-1380.

Conner, D.A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy **63**:48-52.

Conner, D.A. 1983. Response of pikas to playback of geographic variations of the short call. Journal of Mammalogy **64**:336-337.

Conner, D.A. 1985a. The function of the pika short call in individual recognition. Journal of Comparative Ethology **67**:131-143.

Conner, D.A. 1985b. Analysis of the vocal repertoire of adult pikas: ecological and evolutionary perspectives. Animal Behaviour **33**:124-134.

Daniel, J.C., & D.T. Blumstein. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. Animal Behaviour **56**:1517-1528.

Date, E.M. & R.E. Lemon. 1993. Sound transmission: a basis for dialects in birdsong? Behaviour **124**:3–4.

Dearing, M.D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. Oecologia **108**:467-478.

Dearing, M.D. 1997. The function of haypiles of pikas (*Ochotona princeps*). Journal of Mammalogy **78**:1156-1163.

Delgado, R.A. 2007. Geographic variation in the long calls of male Orangutans (*Pongo* spp.). Ethology **113**:487-498.

Dusenbery, D.B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. New York, W.H. Freeman.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist Supplement **139**:125-153.

Esser, K.H. 1994. Audio-vocal learning in a nonhuman mammal-the lesser spear-nosed bat *Phyllostomus discolor*. Neuroreport **5**:1718-1720.

Faraway, J.J. 2006. *Extending the Linear Model with R*, 1st edition. Boca Raton, FL, Chapman and Hall.

Field, A. 2005. *Discovering Statistics Using SPSS*. London, Sage Publications.

Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process*. Huxley, J., A.C. Hardy, & E.B. Ford (eds), London, Allen & Unwin. pp. 71-83.

Forrest, T.G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. American Zoologist **34**:644-654.

Förschler, M.I., & E.K.V. Kalko. 2007. Geographic differentiation, acoustic adaptation and species boundaries in mainland citril finches and insular Corsican finches, superspecies *Carduelis* [*citrinella*]. Journal of Biogeography **34**:1591-1600.

Fotheringham, J.R., P.R. Martin, & L. Ratcliffe. 1997. Song transmission and

auditory perception of distance in wood warblers (Parulinae). Animal Behaviour **53**:1271–1285.

Franken, R.J., & D.S. Hik. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. Journal of Animal Ecology **73**:889-896.

Franken, R.J. 2002. Demograhpy and metapopulation dynamics of collared pikas (*Ochotona colaris*) in the southwest Yukon. MSc thesis. University of Alberta, Edmonton.

Frommolt, K., M.E. Goltsman, & D.W. MacDonald. 2003. Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal. Animal Behaviour **65**:509-518.

Hardouin, L.A., P. Tabel, & V. Bretagnolle. 2006. Neighbour-stranger discrimination in the little owl, *Athene noctua*. Animal Behaviour **72**:105-112.

Hare, J.F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. Animal Behaviour **55**:451-460.

Hare, J.F., & B.A. Atkins. 2001. The squirrel that cried wolf: reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). Behavioral Ecology and Sociobiology **51**:108-112.

Hartwig, S. 2005. Individual acoustic identification as a non-invasive conservation tool: An approach to the conservation of the African wild

dog *Lycaon pictus* (Temminck, 1820). Bioacoustics-The International Journal of Animal Sound and its Recording **15**:35-50.

Hayes, A.R., & N.J. Huntly. 2005. Effects of wind on the behavior and call transmission of pikas (*Ochotona princeps*). Journal of Mammalogy **86**:974-981.

Hunter, M.L., & J.R. Krebs. 1979. Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. The Journal of Animal Ecology **48**:759-785.

Inoue, M. 1988. Age gradation in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). Folia Primatologica **51**:76-86.

Insley, S.J. 2000. Long-term vocal recognition in the northern fur seal. Nature **406**:404-405.

Ivins, B.L., & A.T. Smith. 1983. Responses of pikas (*Ochotona princeps,* Lagomorpha) to naturally occurring terrestrial predators. Behavioral Ecology and Sociobiology **13**:277-285.

Jaeger, R.G. 1981. Dear enemy recognition and the costs of aggression between salamanders. The American Naturalist **117**:962-974.

Karels, T.J., A.A. Bryant, & D.S. Hik. 2004. Comparison of discriminant function and classification tree analyses for age classification of marmots. Oikos **105**:575-587.

Lengagne T, Lauga J, & Jouventin P. 1998. A method of independent time and frequency decomposition of bioacoustic signals: inter-individual

recognition in four species of penguins. Comptes Rendus de L'acedemie des Sciences Serie III: Sciences de la Vie **320**: 885-891.

Lynch, A. 1996. The population memetics of birdsong. In: *Ecology and evolution of acoustic communication in Birds*. Kroodsma, D.E., E.H. Miller (eds), Cornell University Press, London, pp 181–197.

MacDonald, S.O., & C. Jones. 1987. *Ochotona collaris*. Mammalian Species **281**:1-4.

Mager, J. N., C. Walcott, & D. Evers. 2007. Macrogeographic variation in the body size and territorial vocalizations of male common loons (*Gavia immer*). Waterbirds **30**:64-72.

Marler, P. 1955. Characteristics of some animal calls. Nature **176**:6–8.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour **11**:13–39.

Martens, J. 1996. Vocalizations and speciation of Palearctic birds. In: *Ecology and evolution of acoustic communication in birds*. Kroodsma, D.E., E.H. Miller (eds). London, Cornell University Press, pp 221–240.

Mathevon, N., I. Charrier, & P. Jouventin. 2003. Potential for individual recognition in acoustic signals: a comparative study of two gulls with different nesting patterns. Comptes Rendus Biologies **326**:329-337.

Maurello, M.A., J.A. Clarke, & R.S. Ackley. Signature characteristics in contact calls of the white-nosed coati. Journal of Mammalogy **81**:415-421.

Morton, E.S. 1975. Ecological sources of selection on avian sounds. The American Naturalist **109**:17-34.

Mundinger, P.C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: *Acoustic communication in birds*, vol 2. Kroodsma D.E., E.H. Miller, H. Ouellet (eds), New York, Academic, pp 147–200.

Naguib, M., K. Hammerschmidt, & J. Wirth. 2001. Microgeographic variation, habitat effects and individual signature cues in calls of chiffchaffs *Phylloscopus collybita canarensis*. Ethology **107**:341-355.

Nicholls, J.A., & A.W. Goldizen. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. Journal of Animal Ecology **75**:549-558.

Perla, B.S., & C.N. Slobodchikoff. 2002. Habitat structure and alarm call dialects in Gunnison's prairie dog (*Cynomys gunnisoni*). Behavioral Ecology **13**:844-850.

Podos, J. 2007. Discrimination of geographical song variants by Darwin's finches. Animal Behaviour **73**:833-844.

Radford, A.N. 2005. Group-secific vocal signatures and neighbour-stranger discrimination in the cooperatively breeding green woodhoopoe. Animal Behaviour **70**:1227-1234.

Risch, D., C.W. Clark, P.J. Corkeron, A. Elepfandt, K.M. Kovacs, C. Lydersen, I. Stirling, S.M. Van Parijs. 2007. Vocalizations of male bearded seals, *Erignathus barbatus:* classification and geographical variation. Animal Behaviour **73:**747-762.

Robbins, R.L. 2000. Vocal communication in free-ranging African wild dogs (*Lycaon pictus*). Behaviour **137**:1271-1298.

Robisson P, Aubin T, & Brémond J. 1993. Individuality in the voice of emperor penguin *Aptenodytes forsteri*: adaptation to a noisy environment. Ethology **94**:279-290.

Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. Evolution **59**:200-215.

Smith, A.T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology **55**:1368-1376.

Smith, A.T. 1981. Population dynamics of pikas. In: *Proceedings of the World Lagomorph Conference*. Myers, K., & C.D. MacInnes (eds). Guelph, Ontario, Guelph University Press, pp. 572-585.

Smith, A.T. & B.L. Ivins. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Journal of Comparative Ethology **66**:289-308.

Sokal. R.R., & F.J. Rohlf. 1995. *Biometry*, 3rd ed. New York, W.H. Fremman and Co.

Somers, P. 1973. Dialects in southern rocky mountain pikas, *Ochotona princeps* (Lagomorpha). Animal Behaviour **21**:124-137.

Stoddard, P.K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and evolution of acoustic communication in birds*. Kroodsma, D.E., & E.H. Miller (eds), New York, Cornell University Press, pp. 356-374.

Sugiura, H., T. Tanaka, & N. Masataka. 2006. Sound transmission in the habitats of Japanese macaques and its possible effect on population differences in coo calls. Behaviour **143**:993-1012.

Therneau, T.M. & B. Atkinson. 2006. Rpart by Brian Ripley (2006), rpart: Recursive Partitioning, R package version 3.1-33.

Tubaro, P.L., & D.A. Lijtmaer. 2006. Environmental correlates of song structure in forest grosbeaks and saltators. The Condor **108**:120-129.

Tubaro, P.L. & E.T. Segura. 1994. Dialect differences in the song of *Zonotrichia capensis* in the southern Pampas: a test of the acoustic adaptation hypothesis. Condor **96:**1084–1088.

Van Parijs, S.M., P.J. Corkeron, J. Harvey, S.A. Hayes, D.K. Mellinger, P.A. Rouget, P.M. Thompson, M. Wahlberg, & K.M. Kovacs. Patterns in the vocalizations of male harbor seals. Journal of the Acoustical Society of America **113**:3403-3410.

Venables, W. N. & B.D. Ripley. 1999. *Modern Applied Statistics with S-PLUS*. 3rd edn. New York, Springer-Verlag.

Wiley, R. H. & D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology **3**:69–94.

Wiley, R. H. & D.G. Richards. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: *Acoustic Communication in Birds.* D. E. Kroodsma, E. H. Miller, & H. Ouellet (eds), New York, Academic Press, pp. 131–181.

Williams, J.M. & P.J.B. Slater. 1993. Does chaffinch *Fringilla coelebs* song vary with the habitat in which it is sung? Ibis **135**:202–208.

Ydenberg, R.C., L.A. Giraldeau, & J.B. Falls. 1988. Neighbours, strangers, and the asymmetric war of attrition. Animal Behaviour **36**:343-347.

Chapter 4: Conclusions

Introduction

Vocalizations are central to daily interactions between animals and play a major role in social organization (Esser 1994, Robbins 2000, Insley 2000), and possibly community dynamics through shared importance to co-occurring species (e.g. Shriner 1998, Fichtel 2004, Templeton & Greene 2007). Both environmental and social factors are expected to impose strong selection pressures on acoustic signals, yet our understanding of the evolution of animal communication remains limited (Shelley & Blumstein 2004). The evolution of alarm calls in particular has garnered interest because of the apparent risk the caller assumes by drawing attention to its location (Maynard Smith 1965, Hasson 1991). Studies of animal communication have exciting potential to reveal information about many aspects of life history strategies, dispersal, behaviour, and genetics (Mundinger 1982, Martens 1996).

This study contributes to our understanding of the determinants and consequences of vocalizations in mammals generally, and of pikas specifically, by examining 1) sympatric mammal vocalizations as indicators of predators, 2) individual discriminatory abilities, and 3) the sources of geographic call variation between populations and species. In the following sections, I have provided a summary of the main contributions of my thesis,

some limitations of the results, a direct comparison with previous work on American pikas, and potential directions for future studies.

How collared pikas perceive the acoustic environment

When co-occurring species have common predators, the ability to recognize and respond to heterospecifics' alarm calls provides additional information about predator presence (Shriner 1998, Rainey et al. 2004). The research goals of Chapter 2 were to determine the extent to which pikas use the vocalizations of sympatric neighbours to gain information about predators and the threat of conspecifics, and whether they differentiate between callers. I hypothesized that pikas would respond to sympatric calls by increasing vigilance, but would have stronger responses to conspecific calls. Results from playback experiments were generally consistent with these hypotheses, and suggested that mammals use many acoustic and contextual sources of information that should be considered in future studies.

Being attentive to sympatric vocalizations likely confers an energetic benefit and perhaps increased survival. The ability to distinguish between individual conspecifics may allow pikas to make behavioural decisions regarding energy allocation, for example, on foraging over territorial defense. Chapter 2 illustrated the importance of interspecific communication, which has often been overlooked in studies of animal communication. These results support the findings of studies on other species demonstrating that individuals gain

specific information regarding predator type from the calls of conspecifics (Blumstein 1995, Sloan & Hare 2004, Randall et al. 2005), and that animals respond to the alarm calls of heterospecifics in the absence of predators (Nuechterlein 1981, Shriner 1998, Rainey et al. 2004).

One of the challenges I faced in conducting playback experiments with pikas was the uniformity of responses pikas exhibited to conspecific stimuli. Therefore, I used a habituation style experiment to determine that pikas could discriminate between individual callers. This method was limited, however, in that I could only test pika's responses to pairs of individual callers, rather than testing whether they could differentiate between several callers.

Contributions of collared pikas to the acoustic environment

Geographic variation of acoustic signals has generated interest because of its implications for resolving evolutionary and behavioural questions regarding life history patterns, genetic influence on call structure, and animal movement (Mundinger 1982, Lynch 1996, Martens 1996). Two objectives of the study, presented in Chapter 3, were to explore the extent of geographic call variation in collared pikas, and to test whether acoustic adaptation has played a role in species-specific vocalizations. Pika calls varied geographically across populations, and between the two North American species. Collared and American pikas occupy similar habitats, and species-specific calls do not appear to be driven by environmental selection. Therefore, my results suggest

that acoustic adaptation is not a major factor leading to differences in acoustic signatures between populations and species of pikas. Future genetic work on collared and American pikas will help to determine the extent to which this variation reflects evolutionary divergence. In the future, geographic call differences may be used in conjunction with genetic techniques, in order to gain insight into emigration, gene flow, and metapopulation dynamics.

A third objective of Chapter 3 was to explore call characteristics that might carry information on individual identity in pikas. In Chapter 2, I demonstrated that like American pikas (Conner 1985a), collared pikas are able to distinguish between individuals. Potential for individual identity coding values indicated that higher band frequencies vary sufficiently between individuals to allow discrimination.

One of the limitations in the experiment testing the acoustic adaptation hypothesis was that calls were re-broadcasted across relatively short distances through the habitats in order to avoid extensive degradation. This may have limited the true extent of environmental degradation natural calls experience over farther distances. Also, the time and frequency measurements I adopted may not be an accurate representation of how pikas perceive call degradation. However, this experimental design did provide a useful measure of relative acoustic differences, even if the actual magnitude of the effects were underestimated.

Comparison between communication in collared and American pikas

Previous studies have assessed American (Somers 1973; Conner 1982, 1983, 1984, 1985a, 1985b, 1985c; Ivins & Smith 1983; Hayes & Huntly 2005) and Japanese (Kojima et al. 2006) pika calls. These studies demonstrated that American pikas use short calls in both alarm and territorial contexts (Somers 1973, Conner 1985b), that calls show geographic variation which may be a result of separate evolutionary histories or selective pressures (Somers 1973, Conner 1982, Conner 1983), and that American pikas (Conner 1985) and possibly Japanese pikas (Kojima et al. 2006) can discriminate among individuals by call structure alone. These studies highlight the energetic advantages of attending to conspecific calls, and propose genetic divergence as a driver of acoustic variation in American pikas.

Both collared and American pikas are individually territorial during much of the year, but must come together in the spring to breed (Smith 1981, Franken 2002). This and other social interactions are likely facilitated by vocal communication. American and collared pikas live in similar habitats and social environments. Therefore, vocalizations of the two species have been exposed to comparable selection pressures, leading to similar call structures and discriminatory abilities (Table 4-1).

Collared pikas gave one main call during this study, which most closely resembled the harmonically complex single note "short call" given by the American pika (Conner 1985b). A second soft 'contact call' was heard several times when two pikas interacted. Collared pikas appear to have a smaller vocal repertoire than American pikas (Conner 1985b, 1985c) though it is possible that collared pikas give a wider variety of calls when they are below talus, for example in social interactions between mothers and pups. The collared pika call and American pika "short call" both appear to be used in alarm and territorial contexts (Sommers 1973, Conner 1985b). Conner (1985b) found that calls given by an individual American pika in the two contexts could be distinguished by ear, though there was no single characteristic or set of characteristics that distinguished calls among all individuals. I found no evidence that collared pika alarm and territorial calls differ acoustically. Both species may use contextual information when assessing call information (Conner 1982, this study). Both species also exhibited population-level time and frequency differences, likely a reflection of genetic divergence (Somers 1973, Conner 1982, this study), and can discriminate between individual callers (Conner 1985a, this study).

Suggested priorities for future research

Animal communication is an exciting area of research with potential to address a variety of questions regarding life history strategies, dispersal and migration, signal evolution, and behavioural adaptation (Mundinger 1982, Lynch 1996,

Martens 1996). Future studies exploring the extent and importance of interspecific communication in mammals will be integral to our understanding of the complexity of vocal dynamics within communities. We have yet to fully conceptualize the intricacies and contributions of animal communication in structuring community dynamics. Also of interest would be to quantify the energetic advantage of individual discriminatory abilities across different habitat types, and to examine other potential social benefits. High quality recordings in this study reached the maximum frequency level of the recording equipment. Using equipment with ultrasonic recording abilities may reveal that pika vocalizations have a component that extends above 20 kHz. Work that has already been initiated on pika genetics will help to resolve dispersal and movement abilities, and whether call differences reflect genetic divergence. Variations in vocalizations are genetically based in many bird (e.g. Mundinger 1982, Laiolo & Tella 2006) and a few mammal species (Lieblech et al. 1980, Nevo et al. 1987). Future studies combining information on geographic variation in vocalizations with morphological and molecular data could provide a non-invasive, applied component to recording animal calls.

This study has extended our knowledge of the selection pressures associated with giving and receiving acoustic signals. Locally, animals are influenced by other sympatric vocalizations, and calls, as well as behavioural responses to them, may have different characteristics when they evolve in sympatry rather than when other callers are not present. The results presented in this thesis

provide insights into the evolutionary drivers of communication in a small vocal mammal, on local and broad scales.

Table 4-1. Characteristics pertaining to collared (*Ochotona collaris*) and American (*O. princeps*) pika vocalizations.

Characteristic	Collared pikas	American pikas
Social organization	territorial, facultatively monogamous (Franken 2002)	territorial, facultatively monogamous (Smith 1981)
Vocal repertoire	one main call, resembling American pika short call. Another quiet social call heard between individuals (this study)	nine distinct acoustic signals: two types of short call (territorial and alarm), panic call, long call, tooth chatter, trill, cough, and two adult wails (Conner 1985b)
Call function	alarm, territorial (suggested, this study)	alarm, territorial (Somers 1973, Conner 1985b)
Acoustic differences reflective of functional differences	no? (this study)	yes (Conner 1985b)
Geographic call variation	yes; high frequency, frequency of bands 2 and 5, total duration, fundamental total duration, dominant start frequency, and fundamental frequency differed between populations (this study)	yes; fundamental frequency and total duration differed between populations (Somers 1973, Conner 1982)
Discriminate between geographic forms	unknown	yes (Conner 1983)
Significant inter-individual differences	yes, frequency of bands 1-5 (this study)	yes (Conner 1985a)
Individual discrimination	yes (this study)	yes (Conner 1985a)
Attentive to conspecific calls	yes (this study)	yes (Conner 1983, 1984, 1985a)
Attentive to heterospecific calls	yes (this study)	unknown

References

Blumstein, D.T. 1995. Golden-marmot alarm calls. I. The production of situationally specific vocalizations. Ethology **100**:113-125.

Conner, D.A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy **63**:48-52.

Conner, D.A. 1983. Response of pikas to playback of geographic variations of the short call. Journal of Mammalogy **64**:336-337.

Conner, D.A. 1984. The role of an acoustic display in territorial maintenance in the pika. Canadian Journal of Zoology **62**:1906-1909.

Conner, D.A. 1985a. The function of the pika short call in individual recognition. Journal of Comparative Ethology **67**:131-143.

Conner, D.A. 1985b. Analysis of the vocal repertoire of adult pikas: ecological and evolutionary perspectives. Animal Behaviour **33**:124-134.

Conner, D.A. 1985c. The ontogeny of vocal communication in the pika. Journal of Mammalogy **66**:756-763.

Esser, K.H. 1994. Audio-vocal learning in a nonhuman mammal-the lesser spear-nosed bat *Phyllostomus discolor*. Neuroreport **5**:1718-1720.

Fichtel, C. 2004. Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. Animal Cognition **7**:45-52.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. thesis, University of Alberta.

Hasson, O. 1991. Pursuit-deterrent signals—communication between prey and predator. Trends in Ecology and Evolution **6**:325-329.

Hayes, A.R., & N.J. Huntly. 2005. Effects of wind on the behavior and call transmission of pikas (*Ochotona princeps*). Journal of Mammalogy **86**:974-981.

Insley, S.J. 2000. Long-term vocal recognition in the northern fur seal. Nature **406**:404-405.

Ivins, B.L., & A.T. Smith. 1983. Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. Behavioural Ecology and Sociobiology **13**:277-285.

Kojima, N., K. Onoyama, & T. Kawamichi. 2006. Year-long stability and individual differences of male long calls in Japanese pikas *Ochotona hyperborean yesoensis* (Lagomorpha). Mammalia **70**:80-85.

Laiolo, P., & J.L. Tella. 2006. Landscape bioacoustics allow detection of the effects of habitat patchiness on population structure. Ecology **87**:1203-1214.

Lieblich, A.K., D. Symmes, J.D. Newman, & M. Shapiro. 1980. Development of the isolation peep in laboratory-bred squirrel monkeys. Animal Behaviour **28**:1-9.

Lynch, A. 1996. The population memetics of birdsong. In: *Ecology and evolution of communication in Birds*. Kroodsma, D.E., E.H. Miller (eds), London, Cornell University Press, pp 181–197.

Martens, J. 1996. Vocalizations and speciation of Palearctic birds. In: *Ecology*

and evolution of communication in Birds. Kroodsma, D.E., E.H. Miller (eds), London, Cornell University Press, pp 221-240.

Maynard Smith, J. 1965. The evolution of alarm calls. American Naturalist **94**:59-63.

Mundinger, P.C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: *Acoustic Communication in Birds*. Vol. 2. Kroodsma D.E., E.H. Miller E.H., H. Ouellet (eds), New York, Academic, pp 147–200.

Nevo, E., G. Heth, A. Beiles, & E. Frankenberg. 1987. Geographic dialects in blind mole rats: Role of vocal communication in active speciation. Proceedings of the National Academy of Sciences of the United States of America **84**:3312-3315.

Nuechterlein, G.L. 1981. Information parasitism in mixed colonies of western grebes and forster terns. Animal Behaviour **29**:985-989.

Rainey, H.J., Zuberbühler, K. & Slater, P.J.B. 2004. Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society of London, Series B **271**:755-759.

Randall, J.A., B. McCowan, K.C. Collins, S.L. Hooper, & K. Rogovin. 2005. Alarm signals of the great gerbil: acoustic variation by predator context, sex, age, individual, and family group. Journal of the Acoustical Society of America **118**:2706-2714.

Robbins, R.L. 2000. Vocal communication in free-ranging African wild dogs (*Lycaon pictus*). Behaviour **137**:1271-1298.

Shelley, E.L., & D.T. Blumstein. 2004. The evolution of vocal alarm communication in rodents. Behavioral Ecology **16**:169-177.

Shriner, W.M. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Animal Behaviour **55**:529-536.

Sloan, J.L. & J.F. Hare. 2004. Monotony and the information content of Richardson's ground squirrel (*Spermophilus richardsonii*) repeated calls: tonic communication or signal certainty? Ethology **110**:147-156.

Smith, A.T. 1981. Population dynamics of pikas. In: *Proceedings of the World Lagomorph Conference*. Myers, K. & C.D. MacInnes (eds), Guelph, Ontario, Guelph University Press.

Somers, P. 1973. Dialects in southern Rocky Mountain pikas, *Ochotona princeps* (Lagomorpha). Animal Behaviour **21:**124-137.

Templeton, C.N., & E. Greene. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America* **104**:5479-5482.